POPULATION STATUS, REPRODUCTIVE ECOLOGY,

AND TROPHIC RELATIONSHIPS OF SEABIRDS

IN NORTHWESTERN ALASKA

by

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A. Objectives

The objective of RU 460 is to describe important components of the
biology of seabirds in northern Alaska, including relationships among
seabirds, their supporting food webs and the physical environment. To
accomplish this objective we have concentrated on studies of thick-billed
murres *(Uris lomvia)*, common murres *(U. aalge)* and black-legged kittiwakes
(Rissa tridactyla), the most wide-spread, and among the most numerous, of
all seabird species in the region. Moreover, murres and kittiwakes are
easily studied compared to other species, and are sensitive indicators of
environmental change.

B. Conclusions

Our principal conclusions are that numbers of murres at two major
breeding colonies in northern Alaska are declining and that annual vari-
ability is high in a variety of elements of murre and kittiwake breeding
biology. Two possibilities that could account for declining murre numbers
are decreases in **natality** and/or increases in winter mortality. **Annual**
variability in murre and **kittiwake** breeding biology is a function of prey
availability, and is predictable from conditions in the physical environ-
ment during spring and summer.

C. Implications with respect to OCS Oil and Gas Development

Seabirds are very sensitive indicators of environmental change.
They are easily and economically studied by comparison to other **high**-
profile marine vertebrates. Studies of seabirds can yield a great amount
of information on changes in marine food webs important to many top-level
consumers. Such information will be necessary in order to identify possi-
ble effects of oil and gas development on regional marine ecosystems.

II. INTRODUCTION

A. General Nature and Scope of Study

Seabirds occupy top positions in marine food webs and therefore
integrate many elements of regional ecosystems. Among the many species
of seabirds breeding in Alaska , murres and kittiwakes are easily studied
and are sensitive to changes in the environment. Our studies take advan-
tage of these characteristics to examine spatial and temporal differences
in several important marine food webs, and relationships among these food
webs, regional physical processes and seabird biology.

Substantial declines in murre populations that we have documented
during recent years in northern Alaska have demonstrated the need for
a system that will permit future monitoring of colonies as resource
exploration and development increases on Alaska's outer continental shelf.
Therefore, our studies are designed to provide information on the popula-

tion status of murres and on methods to reliably census them, thus **establishing** useful indices of numbers at major breeding colonies in Alaska.

B. Specific Objectives

The specific objectives are to:

1. Census murres and black-legged kittiwakes at major colonies in Northern Alaska.

2. Establish permanent census plots for monitoring numbers in future years.

3. Examine sources of variability in census methodologies that affect the bias and precision in estimates of numbers.

4. Determine levels of reproductive success and breeding **phenol**ogies of murres and kittiwakes.

5. Measure growth rates of kittiwake chicks.

6. Collect specimens of murres and kittiwakes for food habits information, and as a way to sample local marine fishes and invertebrates.

7. Obtain data **on** other species of seabirds that would provide useful information on regional marine ecosystems.

C. Relevance to Problems of Oil Development

The success of **OCSEAP** will depend in part on the ability to detect changes in marine biological systems and, in part, on the ability to separate naturally occurring changes from changes that might result from resource development in Alaskan waters. **OCSEAP** sponsored studies of **sea**birds in the Bering and **Chukchi** Seas have shown that population parameters such as numbers, breeding **phenology** and reproductive success can vary considerably between years. Such marked natural variation could make it difficult to determine if developmental activities were involved in biological changes that might be detected in future years.

Our studies have shown that the annual variability in seabird biology is not random, but is predictable from annual changes in the physical environment and in regional food webs. Information of this kind is relevant to problems of OCS development because it provides the means to more clearly differentiate between natural phenomena and changes resulting from resource development. This aspect of our work is acquiring added importance because of the recent declines in murre numbers that we have documented at two major colonies, one in the eastern **Chukchi** Sea and the other in the northeastern Bering Sea.

Seabirds are appropriate species **to** study not only because they are sensitive indicators of changes in the environment, but also because they are relatively easy to study, especially by comparison to other high

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profile marine vertebrates such as seals and whales. They also offer an
excellent means of sampling lower trophic levels that often defy scientific
sampling methodologies. Therefore, seabird studies can provide a great
amount of relatively inexpensive information on marine ecosystem dynamics.
The monitoring of seabird populations at strategic locations in Alaska may
be one of the most efficient ways of detecting significant changes resulting
from OCS development.

III. CURRENT STATE OF KNOWLEDGE

The first serious attempt to study a large seabird colony in north-
western Alaska was made by L.G. Swartz at Cape Thompson in 1959-1961. We
returned there in 1976, and upon completing that first field season we were
faced with two interesting questions. They were 1) What happened to all the
murres, and 2) What happened to all the kittiwakes? Murre numbers were about
half large as in 1960, and instead of laying nearly two eggs per clutch,
the majority of kittiwakes failed to lay any eggs at all.

Because other species of seabirds that nest at Cape Thompson were few
in number and we saw little change in their populations compared to 1960,
we devoted most of our time in the following years to studies of murres and
kittiwakes. In this report, our current state of knowledge, we describe
changes we saw in murre and kittiwake populations at Cape Thompson and other
colonies in northwestern Alaska in the years following 1976, and discuss
reasons for the changes including man-induced and natural changes in the
environment.

IV. STUDY AREAS

The locations of seabird colonies visited during this study are shown
in Figure 1. Also shown is the location of the Owalit Mountain study area
on St. Lawrence Island which we visited in 1981.

Details concerning the colonies at Bluff, Cape Thompson and Cape Lisburne
have been reviewed in our previous annual reports. Additional information
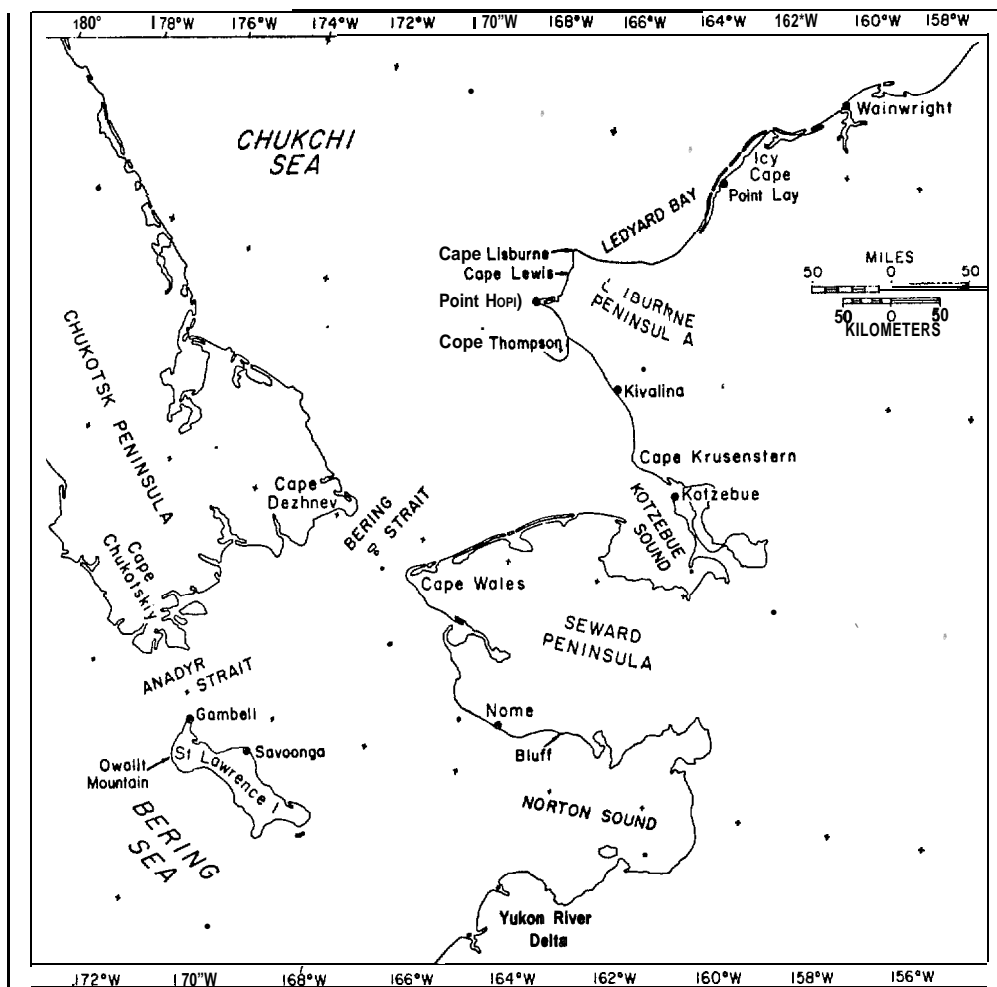on St. Lawrence Island can be found in our annual report for the FY81 field
season.

Figure 1. Study areas in northwestern Alaska.

Cape Thompson

Swartz (1966) first censused the murres at the Cape Thompson colonies in 1960. In conducting the census, he subdivided each of the five colonies into census plots to facilitate counting and recorded the boundaries on photographs **(Swartz,** unpublished data). Plot boundaries were generally defined in accordance with geomorphic features such as cracks and deep ravines. In 1961, Swartz's field crews counted Colony 1 three times and Colony 4 once as well as some of the census plots at the other three colonies.

In each census of murres that we conducted at Cape Thompson we generally used the same plot boundaries as did **Swartz's** field crews. The principal exception was at Colony 5 in 1976 when we lacked photographs showing the original plot designations. In addition, in several instances we had difficulty discerning the boundaries in the photographs and counted adjacent plots as a single unit. In 1979 all five colonies *were* censused on 7 or 8 August; several additional counts of Colony 1 and randomly selected plots at the other four colonies were made during the incubation and chick periods.

All censuses at Cape Thompson have been made between the completion of egg-laying and the onset of sea-going of chicks , **i.e.,** within the appropriate period for censusing as defined by Birkhead and Nettleship (1980). In 1979 at Cape Thompson some of the additional counts were made either shortly before the completion of egg-laying or shortly after the first sea-going of chicks. Here we include any plot counts made during the period commencing one week before the day hatching was first **observed** and end ing one week after the first date chicks successfully left the cliffs. We define this interval as the "Census Period". Lloyd-s (1975) daily counts of common murres indicate that numbers are likely highest and fluctuate least from day to day during this period.

The techniques of counting murres at Cape Thompson were similar but not identical among years. Typically two or three observers counted each plot with the aid of binoculars from a small boat anchored offshore. However, in 1960 most of the plots at higher elevations at Colony 5 were counted from vantage points along the top **of the** cliffs. In 1976 and 1977 these plots, like all other plots, were counted from a boat anchored offshore. In 1979, observers boat-based and land-based counted some of these plots simultaneously to compare the two methods.

Usually observers have estimated numbers by tens, intermittently counting ten individuals to maintain accuracy. However, at Colony 5 in 1960 and 1976 all boat-based esimates were in increments of 100 rather than 10.

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Both thick-billed murres and common **murres** breed at Cape Thompson and occur in varying proportions throughout the five colonies (Swartz 1966). Although one of **Swartz's** field assistants differentiated between the two species in his boat-based counts, no observers in our field crews have done so successfully. All counts reported here are of the two species combined.

Cape Lisburne, Cape Lewis, St. Lawrence Island

The procedures for **censusing** murres at Cape Lisburne and Cape Lewis have been comparable to those at Cape Thompson. Two or three boat-based observers have conducted the counts and, except in 1976 at Cape Lisburne when observers estimated numbers by hundreds, observers have estimated numbers by tens. Complete censuses were conducted at Cape Lisburne only in 1976 and **1977. In** 1978 only six of the 75 plots were counted. In 1979 and 1981. these six plots and four additional plots were counted. Cape Lewis was censused completely **in** 1977 **and** 1981. As **at** Cape Thompson, no differentiation between the two murre species was made in any of these censuses.

Murres on **St.** Lawrence Island have never been censused completely. In 1981 we counted murres at six colonies but did not count those at the remaining four colonies at the east end on the island. **We counted** the **Owalit** Mountain **colony** on 24 July. Previously **S.R.** Johnson (unpublished data) counted this colony on 14 August 1972, and two observers counted the murres there on 26 July 1976 (Searing 1977).

Bluff

Common murres so vastly outnumber thick-billed murres at Bluff (**Drury** *et al.* 1981) that counts there can **be** considered as counts of common murres only. Each census at Bluff has been conducted by one or more boat-based observers. Until 1980 observers counted from a boat moving slowly past the cliffs rather than anchoring at each plot. Beginning in 1980 field crews anchored the boat at each plot before starting the counts. Before 1980 field crews **esimated** the numbers of murres flushing from the cliffs in response to the approaching boat as well as counting those remaining on the cliffs. In contrast **field** crews at Bluff in **1980** and **1981,** and in all years at the other study colonies, have simply waited several minutes to begin counting a particular plot until any murres that had flushed returned **to** the cliffs.

We first participated in censusing murres at Bluff in 1978 and have used the data presented by **Drury** *et* al. **(1981)** for earlier years. Several censuses at Bluff have been conducted outside of the Census Period, and we do not consider them here. Little information on **phenology** was available for 1975; we used **only** the **1** August census and excluded the 4 July and 8 September censuses which fell outside of the Census Period **in** all other years at Bluff. At least two censuses were conducted within the Census Period at Bluff in each year from 1976 through 1981.

At Bluff, but not at the other study localities, a variation of Birkhead and **Nettleship's** (1980) "full-scale method" for determining population status has been used. Numbers of common murre chicks hatching and successfully going to sea have been determined on productivity plots.

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Because plot choices and boundaries were refined as the study progressed and were not finalized until 1977, we have followed the procedure of Drury et al. (1981) and express hatching success as a ratio between the total number of eggs hatching and the average number of individuals in adult plumage present on the plots (k″) and sea-going success as a ratio between the total number of sea-going chicks and the average number of individuals present on the plots (k″). These ratios are similar to a k-value (e.g., Birkhead 1974) which is the ratio between the total number of eggs laid (number of breeding pairs) and the average number of individuals on study plots .

Compensation of Census Results

Numerous studies have documented marked diurnal variation and daily variation in numbers of murres present on the breeding cliffs (e.g., Swartz 1966, Lloyd 1975. Birkhead 1978a, Slater 1980). Consequently, Birkhead and Nettleship (1980) recommended that counts of individuals be made on selected study plots during the same time each day for five to 10 days during the Census Period. However, as Birkhead and Nettleship noted, a key assumption in the use of study plots is that numeric changes on those plots reflect changes in numbers in the whole colony. Rather than accepting this assumption we have counted the entire colony whenever possible. At Bluff a complete census requires only several hours, and two or more censuses at the same time of day have been conducted in each year since 1976, negating the effects of diurnal variation in attendance in comparisons of census results and permitting quantification of daily variation in attendance. At the larger colonies (Cape Thompson and Cape Lisburne) repeated complete censuses have not been possible and a different approach has been taken.

Swartz (1966) introduced a technique of compensating for diurnal variation in attendance and we describe our modification of the technique here. Observers stationed onshore count certain areas (compensation plots) of the colony repeatedly at regular intervals (e.g., hourly) while the census is being conducted by the boat-based observers. At Cape Thompson and our other study colonies we have noted a bimodal pattern in daily attendance of murres with peak numbers occurring in the early morning and late evening. Continuing the counts on the compensation plots until evening peak numbers are ascertained permits adjustment of counts on census plots made earlier in the day to that peak. To calculate the number of murres that would be expected on each census plot at the time of the evening peak, we multiplied the raw count at time t, averaged between or among observers, by the maximum evening count on the compensation plots and divided by the count on the compensation plots at time t. An assumption of this procedure is that the diurnal pattern of attendance on the compensation plots accurately reflects that on the census plots .

At Cape Thompson in 1979 all census counts were coupled with 24-hour counts of compensation plots. In 1960, 1976, and 1977, however, counts of compensation plots at Cape Thompson were not always made in conjunction with the censuses. If compensation counts were not made on the day a particular census plot was counted, or if the compensation counts did not continue through the evening peak in numbers, compensation for diurnal

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variation was made on the basis of all counts during the Census Period on compensation plots in that year. We first expressed each hourly count as a proportion of the evening maximum that day and then averaged **values** from all days counts were made for a particular hour of the day. Thus census counts mad e on days when no compensation plots were counted were compensated in relation to the average diurnal pattern of attendance during the Census Period in that year.

In 1979 at Cape Thompson we made several counts in addition to those during the census. We randomly chose and counted three plots at Colony 2 and one plot at Colony 3 four times during the Census Period . We counted five plots on Colony 2 on 17 August, and field crews counted four plots on each of Colonies 3, 4, and 5 on 11 August. Colony 1 was censused completely three times and Colony 4 once in addition to the censuses on 7 August . These counts provide a basis for compensation of the **census** results in that year for daily variation.

Once all counts of census plots were compensated for diurnal variability, **we** compensated results on the day of the census for daily variation within the Census Period. All plot counts for a particular colony made on a particular day were summed, and the sum was then expressed as a proportion of the census total for those plots. The results for all days that counts of census plots were made, including the day of the census, were then averaged, providing a correction factor for the departure of the census figure from the daily average **in** numbers during the Census Period.

At Cape Lisburne counts of compensation plots were made only in 1977. The diurnal pattern **of** cliff attendance in that year was therefore used as a basis of diurnal compensation in later years. Repeated counts of census plots at Cape Lisburne were made only in 1981 when six plots on the west side of the colony were counted twice. Thus compensation **of** the census results for daily variation at Cape Lisburne was possible only in 1981. No counts of compensation **plots** were made at the time of the census in any year at the **Owalit** Mountain colony, and we report only the raw census results for that colony.

Numerous observers have conducted the field work. We have made no estimates of personal handicaps, as we have no basis for determining which observers estimated numb ers most accurately. Except on small, easily viewed plots the count obtained by each observer should be considered an estimate of the number of murres visible from that vantage point, rather than a true count. In reporting the results here we have computed the mean of simultaneous counts by different observers for each plot and have then summed the results for all plots in each colony.

Several studies have shown that weather influences the number of murres present on the cliffs (e.g., **Birkhead** 1978, **Slater** 1980). Although we have not quantified the effects of weather in the present study, by necessity all boat-based censuses have been conducted in similar weather conditions, i.e., in conditions of calm or light winds, **calm** seas or light swells, no precipitation, and no fog obscuring the cliffs. Tidal fluxes are slight throughout the region, precluding a relationship between tidal stage and numbers of murres **present** on the cliffs like that noted elsewhere by **Slater** (1980).

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As noted earlier, 18 of the upper plots at Colony 5 at Cape Thompson were censused from the top of the colony in 1960 but from a boat at sea in later years. In 1979 we evaluated differences between these techniques by simultaneous counts by boat-based and land-based observers at eight of these plots. The ratio between the land-based and boat-based totals for the eight plots provided a correction factor for boat-based counts of those 18 plots in 1977 and of the remaining ten plots in 1979. Since plot designations at Colony 5 in 1976 differed from those in 1960, we used the ratio between the corrected 1979 total and the boat-based 1979 total as a correction factor to adjust the 1976 total. Thus our compensation for counting location adjusts boat-based counts between 1976 and 1979 so that they are comparable with any land-based counts in 1960.

Modeling of Population Fluctuations

Birkhead and Hudson-s (1977) data on survivorship, age at maturity, and age-related cliff attendance, in connection with the data on numbers and reproductive success at Bluff, provide a basis for modeling changes in population numbers that would be expected to result from annual variations in reproductive success. First we determined the relationship between climatic conditions during the breeding season and reproductive success at Bluff for the years 1975-1979 using polynomial regression analysis (e.g., see Zar 1974). Secondly, we used the resultant regression equation to predict reproductive success from 1942 through 1974, years that climatic data were available but no studies of murres were conducted , and 1980, when our visit to the colony was brief and predated the period of sea-going of chicks. Thirdly, we constructed a population model based on a modified Leslie matrix, lumping all adults into a single age class (e.g., see Mertz 1971), but maintaining yearly age classes up to the age of maturity. Thus each cohort could be tracked individually until the age of maturity. Using the average predicted reproductive output for the years 1942-1980 and Birkhead and Hudson's (1977) figure of 0.915 for adult survivorhsip, we determined the value for subadult survivorship (0.339) which would result in a stationary population. Fourth, we ran the model with those particular values of survivorship inputing the predicted reproductive success in each year in succession. Due to the multi-year lag between the time chicks leave the cliffs and the time they return as subadults or adults (see Birkhead and Hudson 1977), the model can be used predictively as well as providing a simulation of observed trends. The model provides a test of the hypothesis that numeric variations are due to variability in natality, i.e., to conditions during the breeding season.

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Cape Thompson

The timing of the censuses at Cape Thompson and breeding **phenology** during the years complete censuses were mad e are shown in Table 1. Completing the census generally required several days, ranging from two days in 1979, when two crews simultaneously counted different portions of the colonies, to 14 days in 1960.

Table 2 summarizes the census results at Cape Thompson. Both the raw counts and compensated results indicate that numbers declined markedly between 1960 and 1976 and that the decline continued between 1976 and 1979. The decline occurred primarily at Colony 5, the only colony where fewer murres were counted in each successive census. Although numbers at Colonies 1-4 were also lower in recent years than **in** 1960, there was no clear trend in numbers at those colonies between 1976 and 1979. To evaluate the null hypothesis that there were no **intercolony** differences in the degree of numeric change among years, we conducted a Chi Square Test for differences in probabilities (Conover **1980:153**) using the standardized results. The test statistic was highly significant (T = 12,096; v $^=$ **12**, **P < 0.001**). Significantly fewer murres were present at Colony 5 in 1977 and especially in 1979 than would be expected if numbers there had changed at the same rate as at the other four colonies. Thus the **murre** populations have apparently consolidated at Colonies 1-4 as the decline in numbers has progressed.

Cape Lisburne, Cape Lewis, and St. Lawrence Island

Complete censuses of the Cape **Lisburne colony** were made in 1976 and 1977 ; counts of portions of the **colony** were made **in** 1978, **1979,** and **1981** (Table 3). All counts were made during the Census Period. Results standardized for time of day suggest that **murre** numbers at Cape **Lisburne** were highest in **1979. In** that year counts were made in the **afternoon** rather than in the evening as in other years. Because the **1977** counts at compensation plots showed that numbers were low in the afternoon and peaked in the evening, compensation according to those counts greatly increased only the 1979 results. Because **(1)** the assumption that the 1977 diurnal patterns of **cliff** attendance **is** typical of all years may not be **valid** and (2) no compensation for **daily** variation **in attendance** at Cape **Lisburne** could be made except for **1981,** the apparent differences among years at Cape Lisburne may be spurious.

There have been **only** two censuses at Cape Lewis **and** the results were similar. Counts, averaged between observers, were **19,130** in 1977 and 20,564 in 1981. **No** compensation of these counts has been made. There is insufficient evidence **to** indicate that numbers have changed significantly at either Cape Lisburne or Cape Lewis, but certainly there is no evidence that numbers at these colonies have declined in synchrony with the declines at Cape Thompson.

On St. Lawrence Island in 1981 we counted approximately 329,000 murres at six of ten colonies where they are known to nest. The other four

colonies contain about 30,000 to 60,000 murres (F.H. Fay, pers. comm., Drury *et al.* 1981). At the Owalit Mountain Colony the average of the counts of two observers was 33,955 murres. S.R. Johnson (unpubl. data) counted 31,830 murres there in 1972,. In 1976, the average of the counts of two observers was only 15,635 murres (Searing 1977). Searing (pers. comm.) included murres flying in front of the cliffs and those on the water as well as murres on the cliffs. Therefore, the number of murres on the cliffs was even lower than that reported for 1976. Neither diurnal nor daily variation in attendance patterns of murres were quantified in conjunction with any of the colony counts on Owalit Mountain. Although these sources of variation can be substantial, the dip in numbers in 1976 was probably the result of unusually cold weather. In 1976 snow persisted as late as 14 June on the ledges normally occupied by murres, and egg-laying did not peak until early July (Searing 1977) about two weeks later than usual (Fay and Cade 1959). The low count in 1976 could be due to the absence of many murres that would normally occupy breeding ledges or to reduced time on the ledges. No data are available to evaluate such possibilities.

The Owalit Mountain Colony constitutes less than ten percent of the murres on St. Lawrence Island. Because that colony is the only one with a history of counts, we do not know if parallel fluctuations in numbers have occurred at other colonies on the island or if they were localized to the Owalit Mountain Colony. The opinion of residents of Gambell (e.g., L. Iyakitan, pers. comm.) is that murres have been increasing in numbers. In 1981 Lane Iyakitan showed us areas in Boxer Bay, near Southwest Cape, where murres have nested only in recent years.

Bluff

At Bluff two or more censuses were made in each year from 1975 through 1981. Several censuses occurred either before eggs began to hatch or after sea-going of chicks began. Table 4 summarizes the census dates relative to breeding phenology, indicating which dates fell within the Census Period. Two or more censuses were conducted within the Census Period in all years but 1975.

Numbers of murres at Bluff declined between 1975 and 1981 (Table 5). A significant downward trend is evident (Spearman's $r = -0.96$, $n = 7$, $P < 0.005$). None of the counts in 1980 or 1981 exceeded the counts in 1975-1977.

On 11 July 1976, nine days before the start of the Census Period, only 20,779 murres were present on the cliffs. This count is substantially lower than those during the Census Period that year and perhaps indicates that the counts during the Census Period were overestimates of the average number of murres on the cliffs that year. However, even if the census on 11 July is included in the results for 1976, the average of the censuses in that year would equal 40,448, which is higher than the mean of the counts in any subsequent year. Therefore, the census results, although quite variable within years, do indicate that numbers declined at Bluff between 1975 and 1981.

In addition to the complete boat-based censuses at Bluff we conducted

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counts on several days during the Census Period at two locations, Stake 10 and Stake 15, from observation sites at the top of the cliffs. Results of all counts which we started at 1700 h (Bering Daylight Time) are listed in Table 6. At Stake 10 fewer murres were present in 1980 than in either 1979 and 1981. More murres were present at Stake 15 in 1981 than in either 1979 or 1980. Thus, in contrast to the census figures, these results suggest that the decline in numbers of murres at Bluff did not continue through 1981. These counts are certainly more precise and accurate than boat-based counts but these two stakes represent only a small fraction of the cliffs which the murres use at Bluff. Changes at these two locations therefore may not be representative of numeric changes at other locations within the colony.

Table 5 shows reproductive as well as census data for Bluff. Our observations suggest that reproductive success was quite low in 1975 and 1976 and then increased at least through 1979. In 1980 and 1981 data were not obtained on "fledging" (sea-going) success. Reproductive success was also probably quite high in 1980, but in 1981 it was probably comparable to that in 1977.

Major changes between years in the past decade in the food habits of murres and black-legged kittiwakes (Sections Vb-VIIb) and reproductive success of kittiwakes (Sections Vc-VIIc) were associated with changing environmental conditions. We lacked detailed data on annual variation in water temperatures in Norton Sound. However, Niebauer (1.980) showed that water temperatures and air temperatures (heating degree days) in the Southeastern Bering Sea are positively and significantly correlated. Therefore, we examined the relationship between reproductive success and air temperatures. Only limited climatic data were available for Bluff. Climatic data for Nome, 80 km west of Bluff, correspond quite closely to those at Bluff and are far more extensive. We therefore used the climatological records from Nome to examine the relationship between reproductive success and air temperature. Since the number of sea-going chicks in early August is likely related to conditions during the previous several months, we chose cumulative heating degree days during the months of April through July as our measure of air temperature during a two-month pre-breeding period and the two-month reproductive season.

We examined the relationship between reproductive success and air temperature using polynomial regression analysis. A quadratic equation provides an excellent fit, indicating that our measure of air temperature accounts for 95% of the variance in reproductive success (Figure 1). Thus air temperatures apparently are closely coupled with factors such as sea-surface temperatures and food availability, which probably more directly influence reproductive success.

Modeling the Relationship Between Reproductive Success and Population Numbers

Because reproductive success is highly correlated with temperature we examined the historical records of summer climate at Nome. During the period from 1959 to 1977 only three summers were warmer than normal; the summers of 1975 and 1976 were exceptionally cool (see Figure 2). Thus reproductive success likely was low in most years from 1959 to 1977. To

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address the relevance of poor reproductive success to the decline in numbers at Bluff in recent years, we developed a model to simulate changes in population numbers of common murres at Bluff in relation to variability in reproductive success. Values for parameters in the model were either calculated from data collected there since 1975 or were obtained from studies of common murres elsewhere (see Table 7).

Data on heating degree days at Nome were available from 1942 through 1980. We used the quadratic equation (Figure 1) to predict reproductive success in each year during that period. Average predicted success in that 39-year period was 33.4 sea-going chicks/100 individuals. Assuming a stationary population between 1942 and 1980, the one remaining unknown, survival of subadults, from the time they leave the cliffs as chicks until they begin to breed, can be determined analytically from the tabulated values for adult survivorship, age at maturity, and average reproductive success. The values of age-specific subadult survivorship of second-year, third-year, and fourth-year subadults were generalized from Birkhead and Hudson's (1977) results which show that survivorship of subadults increases with age. Survivorship of first-year birds was set to 0.5545 so that the product of age-specific survivorship values of subadults would equal 0.339, the value of overall subadult survivorship (Table 7).

Our counts of murres at Bluff, as elsewhere, include not only incubating and brooding adults, but also their off-duty mates, failed breeders, non-breeding adults, and subadults (see Birkhead 1978a). The proportion of individuals present during the censuses to the total number of individuals using the cliffs was calculated using the tabulated k-value and the values of age-specific use of the ledges shown in Table 7. An assumption implicit in this calculation is that the variance in the number of individuals present among counts reflects the variable presence of adults as well as subadults. Slater (1980) demonstrated considerable diurnal variability in the presence of off-duty mates on the cliffs.

The values shown in Table 7 produce a population which is stationary in numbers. Inputing the annual values of predicted reproductive success, rather than average predicted reproductive success, during the period 1942-1980, we then simulated population changes which would be expected during that period if variability in reproductive success has been the key to changes in numbers we have observed at Bluff. In conducting this analysis we set the initial (1942) population size so that predicted and actual population size in 1976, the first year at least two censuses were conducted, would be equal.

Results of the simulation (Figure 2) suggest that numbers of murres at Bluff were high in the early 1960-s, declined in the late 1960's following a series of cold summers beginning in 1959, and declined further in the late 1970's. The predicted trend between 1975 and 1981 is quite similar to that observed (Table 5). The correlation between observed and predicted numbers is positive and significant (Spearman's p = 0.86, n = 7, P< 0.01).

The model, like the trend at Stake 10 (Table 6), suggests that population numbers decreased through 1980 but then began to increase in 1981. As noted earlier, numbers at Stake 15 were equivalent in 1979 and 1980 but higher in 1981. Stake 15 is apparently primarily a club area;

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relatively few **ledges** will safely accommodate an egg there and variability **in** numbers of **murres** is relatively high. In 1979 the coefficient of variation in the counts at 1700 **h** during the Census Period **at** Stake *15 (14.5%)* was more than twice that at Stake 10 *(6.8%)* even **though** the counts at these two areas were conducted simultaneously (except for one additional count at Stake 10). Although Birkhead and Hudson **(1977)** defined clubs as aggregations of **murres** on tidal rocks, the **slight** tidal fluxes in the region of our study apparently preclude such sites for clubs. Clubs at our study colonies probably form in areas of low breeding density on the cliffs. Because **clubs** are comprised primarily of **subadults,** particularly **two-year-olds (Birkhead** and Hudson 1977), an increase in population numbers would occur in areas used by clubs before it would occur on the breeding ledges. Thus the trends of numeric change at Stakes **10** and **15** coincide with those expected **if** variability in reproductive success has been the key to changes in overall numbers at **Bluff in** recent years.

The magnitude of the decline in the **late 1970's** predicted by the model was much less than that indicated by the census results. This discrepancy may indicate that either (1) **interannual** variability in reproductive success was **only** partially responsible for observed changes in numbers from 1975 through **1981, or** (2) the **actual** decline has been far **less** pronounced than is suggested by examination of the annual mean counts **only.** Certainly **intra-annual** variation in census results has been high (Table 5); consequently the **sample** means derived from two or three censuses have been rather imprecise estimates of mean numbers on the cliffs. However, if these estimates are accurate (unbiased), factors in addition to summer conditions probably are implicated in the declines.

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VIIa. MURRE NUMBERS - DISCUSSION

In the following discussion we first address **intralocality** (Cape Thompson only) and then **interlocality** variation in changes in numbers and then factors responsible for such changes. The theoretical basis is **Fretwell's** (1972) theory of habitat selection; we hypothesize that a **subadult** will prospect at several colonies and several areas within those colonies and will subsequently establish a breeding site at the colony, and at the particular area within that colony, which will maximize its probability of reproductive success.

Although data are lacking on **intercolony** movements of **subadult murres,** detailed studies of other seabirds, e.g., **fulmars** (*Fulmarus glacialis*) **(Coulson** and Horobin 1972) and black-legged kittiwakes **(Coulson** and **Wooler** 1976), indicate that juveniles and **subadults** disperse widely from their breeding colonies and may visit several colonies before selecting a breeding site to which they likely will return in each subsequent breeding season. Thus **intercolony** transfer of individuals does occur **in** other species of seabirds and results from nest site selection away from the natal colony by at least some propsecting subadults.

Birkhead (1977) showed that year-to-year fidelity of adult murres to their nest sites is high; 95% of his sample of banded and returning adult common murres returned to the same portion of the breeding ledge that they occupied the previous year. However, he also hypothesized that nest site tenacity would be reduced if reproductive success is poor and cited Johnson-s (1938) findings that adults abandoned nest sites on ledges that were subject to heavy predation by gulls and resettled elsewhere in the same colony in the same year. Thus, movements of adults from one area to another within a locality normally is rare but could be expected to increase during periods of population decline as sites in more suitable portions of the colony become available.

Intralocality Variation: Cape Thompson

The census **results** at Cape Thompson indicate a marked decline in murre numbers between 1960 and 1976 and a continuation of this decline through 1979 when censuses were last conducted there. The decline was not spread uniformly across the five colonies, suggesting either differences in **natality** or survivorship among the colonies or a consolidation of the population at the more suitable colonies as the overall decline progressed.

Birkhead (1974) showed that most adult mortality is restricted seasonally to the nonbreeding season. Because murres breeding **at** the Cape Thompson colonies likely overwinter south of the ice edge in the southeastern Bering Sea (Irving *et al. 1970,* **Shuntov** 1974, Divoky 1978), individuals from the five colonies certainly mingle on the wintering areas and are thus subjected to the same mortality factors.

Swart z (1967) found murres from the Cape Thompson colonies feeding up to 100 km or more away from the colonies. Because (1) the colonies span only 11 km of coastline, (2) we have observed **murres** from the various colonies depart in the same flocks to foraging areas and **returning** together from foraging areas, and (3) we have observed seasonal changes in flight

directions of murres flying to and from foraging areas, there is no evidence that **murres** occupying sites *in* the five colonies differentially exploit food resources or vary consistently in their proximity **to** such resources. To the extent that reproductive success is food-limited, reproductive success should not vary systematically among the five colonies.

In terms of both absolute and relative numbers the decline has been far greater at Colony 5 than at the other four colonies. As noted in the description of the Cape Thompson colonies, the rock is much softer and more extensively fragmented at Colony 5 than elsewhere. Although numerous minor **rockfalls** and one major **rockfall** occurred at the other four colonies between 1976 and 1979, such occurrences were infrequent compared to the almost incessant rock showers and occasional rock slides at Colony 5. As well as breaking eggs and killing chicks, such slides do kill adults (personal **observations**). Thus the major decline at Colony 5 **could** be due to a lack of **subadult** colonization of this relatively unsuitable colony and possibly to transfer by already-established adults from Colony 5 to the other four colonies as more suitable areas in the other colonies became available during the overall decline.

We were unable to distinguish **the** two murre species in our census counts. **Swartz** (1966) estimated that thick-billed **murres** comprise 81% of the **murres** using Colonies 1 and 5, 60% of those using **Colony** 3, and less than 50% of those using Colonies 2 and 4 (49% and 43%, respectively). Although the major decline **at** Colony 5 could indicate that the overall decline was due to a decline in numbers of thick-billed **murres only**, the compensated census results (Table 2) indicate that the decline was also both absolutely and relatively high at Colony 2, where common **murres** outnumbered thick-billed murres in 1960 **(Swartz** 1966). Thus the decline **in** overall **murre** numbers probably reflects a decline in numbers of both species.

Common murres are larger, heavier and more agile than thick-billed **murres** (Spring 1971) and are dominant in aggressive encounters for breeding sites at colonies where both species breed (Williams 1974). **Belopolski** (1961) showed that during a period when common murre numbers increased in the Murmansk region, common murres gradually displaced thick-billed **murres** from the broader ledges. Conversely it could be expected that thick-billed **murres** would again occupy broader ledges during a period of decline in the common murre population. Thus the spatial pattern of population decline among the Cape Thompson colonies is consistent with **a** reduction in numbers either of both species or only **of** common murres accompanied by a consolidation of the thick-billed murres in relatively suitable breeding areas.

Interlocality Variation in Numeric Changes

The declines at Cape Thompson have been paralleled at Bluff, where common murres predominate, but not at the other mixed species colonies at Cape **Lisburne** and St. Lawrence Island. The declines in recent years at Bluff can be explained, at **least** partially, by relatively cool summers and associated poor reproductive success **in** the past two decades. Compared to the **climatological** data base for Nome, there are few weather data available

for Cape Thompson; Allen and Weedfall (1966) showed that summer air temperatures there are well correlated with those at Kotzebue but are somewhat cooler. In turn, Kotzebue temperatures from April through July are highly correlated with those at Nome (heating degree days, r = 0.889, n = 22 (1959-1980), P< 0.01). Thus, interannual fluctuations in air temperatures at Cape Thompson and Bluff likely have occurred in parallel.

We lack detailed data on reproductive success at Cape Thompson and only can infer annual differences from annual variation in breeding phenology and egg sizes. In a given year common murres and thick-billed murres begin to lay eggs on virtually the same day (Swartz 1966), but the timing of breeding by both species has varied substantially among years (see Table 1). Using the Kotzebue weather data and information on hatching phenology, we found a strong correlation between date of first hatching and late-spring, early-summer temperatures (heating degree days, April-July, Spearman's p = 0.886, n = 6, P < 0.005). Phenology is advanced in warm years. Studies elsewhere (e.g., Birkhead and Nettleship 1981) have shown that reproductive success is higher when breeding is earlier.

Birkhead and Nettleship (1981) also documented a positive relationship between egg size and reproductive success. At Cape Thompson we obtained data on egg sizes of both murre species on several accessible ledges in 1977 and on a subset of those ledges in 1979. We grouped the egg volume ($0.50 \times$ length x breadth^2) data by species and year and then conducted a factorial ANOVA. Egg volumes of both species were greater in 1979 than in 1977 (thick-billed murres, 1977: mean = 96.4, s.d. = 9.4, n = 55; 1979: mean = 104.5, s.d. = 10.0, n = 36; common murres, 1977: mean = 107.4, sod. $^-$9.0, n= 16; 1979: mean = 117.3, s.d. = 9.9, n = 5 ; ANOVA Year effect: F = 4.685, V = 1,108, P< 0.033). At Bluff reproductive success was higher in 1979 than in 1977 (Table 5). Thus both the phenology and egg volume data indicate that reproductive success of murres at Cape Thompson has likely paralleled that at Bluff. Consequently, the decline at Cape Thompson has possibly been due to relatively poor reproductive success in association with relatively cool summers in the past two decades.

Air temperatures at Cape Lisburne average several degrees cooler than those at Cape Thompson (Allen and Weedfall 1966) and are well correlated with those at Kotzebue (heating degree days, April-July, r = 0.728, n = 16, P < 0.01). Furthermore sea-surface temperatures measured near Cape Lisburne in July between 1974 and 1981 show a pattern of change similar in direction and magnitude to that of April-July air temperatures at Nome and Kotzebue (see Sections Vb-VIIb). On the basis of the above discussion, a decline in murre numbers would also be predicted at Cape Lisburne, but numbers appeared to remain stationary from 1976 through 1981.

Drury (1979) noted that during periods of general population increase or decline, seabird numbers at some localities may change substantially while those at others remain stationary, and he argued that proximity to food resources is probably a key factor affecting such interlocality variability.

In most years food availability near Cape Lisburne appears to be higher than that near Cape Thompson. Black-legged kittiwakes typically have higher reproductive success, and growth rates of kittiwake chicks are

faster at Cape **Lisburne** than at Cape Thompson (see Sections **Vc-VIIc**). The reasons for these differences are not well understood but are possibly related to physical oceanographic processes that make Ledyard Bay, the region northeast of Cape Lisburne, an especially favorable foraging area (see Sections **Vb-VIIb**). Thus reproductive success of **murres** at Cape Lisburne is probably generally higher than **at** Cape Thompson.

St. Lawrence Island, like Cape **Lisburne,** is favorably situated with respect to foraging areas. Anadyr Strait is an extremely productive region in which enormous numbers of **auklets, murres,** and **kittiwakes** feed **(Bedard** 1969, personal observations). Although kittiwake reproductive success **on** St. Lawrence Island was **similar** to that at **Bluff** and Cape Lisburne in 1981, chicks on St. Lawrence Island grew substantially and significantly faster than did those at Bluff or Cape Lisburne (see Sections **Vc-VIIc**). The **low** count of murres at **Owalit** Mountain in 1976 can **be** related to adverse . conditions early in the breeding season (Searing **1977**). The influence of such conditions **early** in the breeding season on murre numbers during the Census Period indicates that severe conditions can affect census results. However, **Birkhead (1978b)** documented intense competition for breeding sites, and Williams **(1974)** found that prior ownership **plays** a key role **in** contests for sites. Consequently, there is likely a premium on maintaining occupancy **of** a site even in years when the probability of reproductive success is low, and therefore in most years numbers on the **cliffs** probably do provide a reasonable index of population numbers. **In** extremely adverse conditions numbers, as **well** as reproductive **success,** may be depressed.

The declines **at** Cape Thompson and **Bluff** are fundamentally different **than** the apparent short-term change at St. Lawrence Island. At **Bluff** numbers have declined **while** reproductive success has varied and generally increased (see Table 5). Although numbers of **murres** at Cape Thompson were substantially lower in **1979** than in 1977, the data **on** egg volumes and **phenology** suggest that reproductive success *was* greater **in 1979.** Thus the lowest census **total** at Cape Thompson **(1979)** certainly did not occur in conjunction with adverse conditions in that particular breeding season.

Differences among localities in proximity to food supplies likely results in differences in rates of numeric change during a **general** population increase or decrease. Such differences could **result** from differences in reproductive success and **could** be augmented by shifts **to** the more productive colonies. Although **Drury** and **Nisbet (1972)** showed **that** some **adult** herring **gulls** (*Larus argentatus*) nesting **in** colonies characterized by poor reproductive success move to more productive colonies, site tenacity **of adult** murres is extremely high **(Birkhead 1977)** , **and** long-distance relocation seems unlikely. However, movement of individuals prior **to** age at first breeding from **natal** colonies characterized by relatively poor reproductive success to **more** productive colonies certainly is possible. However, documentation of such movements, particularly between major colonies, would be virtually impossible as it **would** require banding of sea-going chicks on a massive scale and detailed searching for banded birds several years later at colonies other than the natal colony.

In summary, the variable patterns in census results for the various colonies are consistent with an overall population **decline,** i.e., the

declines at Cape Thompson and Bluff may reflect declines in **regional** populations of one or both **murre** species rather than localized effects on breeding populations only at those colonies. Examination of factors responsible for those declines should include consideration of factors acting on regional populations as well as those acting on the murres at Cape Thompson and Bluff.

Factors Affecting Population Change

Drury (1979) reviewed several studies documenting the sensitivity of population numbers of seabirds to long-term environmental fluctuations. We have shown that in northwestern Alaska environmental conditions during the breeding season not only fluctuate widely between years but also demonstrate long-term trends. In the 39 year history of reporting of heating degree day data for Nome by the U.S. Weather Bureau and the National Weather Services, the first two decades were relatively warm and the last two decades have been relatively cool (see Figure 2). Because reproductive success at Bluff is strongly and positively correlated with late-spring, early-summer temperatures, recent population declines there are probably related, at least partially, to reduced reproductive success in the early and **mid-1970's,** as our simulation model shows.

At the present time agreement between observed and predicted changes in numbers at Bluff is only in terms of trends; the magnitude of the decline of one percent annually that was predicted by the simulation model (Figure 2) is considerably less than that implied by the census results (five percent annually, 1976-1981, see Table 5). We consider two explanations of this discrepancy. First, the mean of two or three counts is a very imprecise measure of numbers on the cliffs in a particular year because **intra-annual** variation between (among) counts is high. Thus the observed decline could be an overestimate of the true rate of decline. Alternatively. factors affecting mortality could be implicated in the decline.

As noted earlier, Birkhead (1974) showed that mortality of murres occurs primarily in the nonbreeding season. Murres breeding at all colonies in the northern Bering Sea and the **Chukchi** Sea, including those at Bluff, likely mingle extensively at wintering areas in the southeastern Bering Sea (see **Shuntov** 1974). Consequently, overwinter mortality must act on the regional population as a whole rather than differentially on individuals associated with particular colonies **(Drury** 1979). Factors which could reduce survivorship in wintering areas include long-term natural changes, natural catastrophes, and human influences.

Niebauer (1980) summarized the marine climate in the southeastern Bering Sea in the past decade. Beginning in 1973 , a cooling trend led to a decline in sea-surface temperatures to **1.5°C** below the 15-year mean by 1975; sea ice reached its maximum southern extent during the 1975-1976 winter. Between the fall of 1976 and the spring of **1979,** a warming trend occurred and was characterized by annual increases of about 0.7°c in sea-surface temperatures and annual decreases in ice coverage of about ten percent. There are no data on the effect of such variation in winter climate on overwinter survival of murres. Numbers of murres at Bluff and Cape Thompson declined as the warming trend progressed while those at Cape

Lisburne and the Pribilof Islands (see Hunt *et al.* 1981) apparently remained stationary. Although winter climatic conditions could affect survival. we cannot address such a relationship with the available data.

Natural catastrophes in the region, such as the die-off of an estimated 100,000 common murres along the the Alaskan Peninsula in the spring of 1970 (Bailey and Davenport 1972) would result in short-term fluctuations in numbers but not in declines persisting over several or many years.

Studies elsewhere (e.g., Cramp *et* al. 1974, Nettleship 1977) have documented the adverse consequences of oil development and particularly oil spills on murres. Oil development has not yet begun in the Bering or Chukchi Seas. McKnight and Knoder (1979:190) cited two instances of murre die-offs in Alaska which were apparently associated with oiling. Although such events will surely increase as oil development accelerates along the Alaska coast, the declines at Cape Thompson and Bluff in recent years have occurred independently of such events; i.e., oil development cannot be implicated in these declines.

Annually several hundred thousand seabirds have been caught incidentally in the salmon gill net fishery in the north Pacific Ocean (e.g., King *et* al. 1979). This fishery began in 1952 and expanded rapidly in the next several years. Estimates of seabird mortality in the early to mid 1970's ranged between about 250$000 and 750,000 birds annually (King *et* al. 1979). Agreements between Japan and the USSR resulted in a reduction in the fishery in 1977 ; imposition of the 200-mile territorial limit by the United States led to a further reduction in 1978. However, DeGange (1978) estimated that 290.000 seabirds were drowned in drifting salmon gill nets in 1978. Estimates of murre numbers range from 11 percent to 58 percent of all birds caught (DeGange 1978). Tull *et al.* (1972) reviewed the tremendous adverse effect of the salmon gill net fishery on murre numbers in western Greenland. However, in Alaska the fishery operates several hundred kilometers south of the colonies we have studied and principally during the summer months. Thus survivorship age classes returning to the study colonies would be unaffected by the salmon gill net fishery. Birkhead and Hudson (1977) showed that one-year-old common murres did not return and few two-year-olds returned to their study colony. The declines at Cape Thompson and Bluff could be ascribed in part to the incidental salmon catch only if such age classes remained in the wintering areas which overlap the region of the fishery.

Murres are primarily piscivorous seabirds, preying on a variety of small fishes, including young age classes of commercially important species (e.g., Straty and Haight 1979). In some regions, e.g., the North Sea, seabirds and man are competing intensely for a restricted food supply (see Furness 1978). Brown (1980) reviewed the competitive conflicts between seabirds and commercial fisheries and concluded that such conflicts will intensify particularly because fisheries pressure is shifting more and more to species which are central to the food webs of piscivorous seabirds.

Walleye pollock (*Theragra chalcogramma*) appear to be the principal winter food of both thick-billed murres and common murres in the southeastern Bering Sea (Divoky 1978). The pollock fishery in that region

started in the early 1960"s as stocks of yellowfin sole (*Limanda aspera.*) were depleted. Even after overexploitation in the early 1970-S and continued declines in the catch per unit effort **(CPUE),** Bering Sea **pollock** still constitute the most important single species fishery in the north Pacific region **(Bakkala** *et al.* 1981). Thus in the past two decades commercial fisheries pressure on a principal species in the winter diet of **murres** has intensified greatly.

If human exploitation of **pollock** does constitute true competition with murres, overwinter survivors **ip** of **murres** could be reduced. Population numbers of long-lived, low-fecundity taxa such as murres are extremely sensitive to slight alterations in adult survivorship (e.g., see Mertz 1971); reducing survivorship by a few percentage points would result in population declines of the magnitude we have observed at Cape Thompson and Bluff.

The **CPUE** of **pollock** is shown in Figure 3 as are the counts of murres at Bluff. The two-year lag between the decline in the **pollock CPUE** and the decline in **murre** numbers at Bluff would be expected if competition with the **commerical pollock** fishery has reduced primarily survivorship of the youngest age classes because there is a comparable lag between sea-going of chicks and their return to the colony (Birkhead and Hudson 1977). Young **murres** are inexperienced at foraging and would likely be the first individuals to suffer from a decline in food availability.

Although increased overwinter mortality would be experienced by murres from all of the study colonies, numbers at more suitable colonies could remain relatively stationary due to higher reproductive success and possibly immigration of young individuals. Numbers could decrease substantially at less productive colonies at the same time due to lower reproductive success and emigration of young individuals. Therefore, numeric declines at Bluff and Cape Thompson but stationary numbers at Cape Lisburne and short-term fluctuations on St. Lawrence Island are consistent with a regional population decline due to decreased overwinter survivorship. The discrepancy between the observed and modeled rates of decline at Bluff could be the consequence of increased overwinter mortality as well as low reproductive success in recent years.

The simulation model can be extended to provide a prediction of numb ers of murres at Bluff for the next several years because there is a multi-year lag between the time chicks leave the cliffs and the time when they return as **subadults** (Birkhead and Hudson 1977). Because summers have been relatively warm (Figure 2) and reproductive success has been moderate or high since 1978 (Table 5), population numbers at Bluff should increase markedly over the next three years (1982-1984) if variability in reproductive success plays a key role in changes in numbers (see Figure 2). In contrast, **pollock** abundance and the **pollock** CPUE have remained **low** during the same period (see Figure 3; **Bakkala** *et al.* 1981). If competition with **commerical** fisheries is the key factor in the recent decline in murre numbers at Bluff, the decline should continue during the next several years.

TABLE 1. Dates of murre censuses at Cape Thompson in relation to breeding phenology.

Event	Year			
	1960	1976	1977	1979
First Hatching	30 Jul	9 Aug	1 Aug	22 Jul
First Sea-Going	18 Aug	>25 Aug[1]	23 Aug	11 Aug[2]
Census Dates				
Colony 1	17 Jul	6 Aug	11 Aug	8 Aug
Colony 2	27,29,31 Jul 3 Aug	18 Aug	9 Aug	
Colony 3	21-23 Jul	23 Jul	10,12 Aug	7 Aug
Colony 4	15-17 Jul	9 Aug	12 Aug	7 Aug
Colony 5	1,2,4,12 Aug	19 Aug	13,14,17 Aug	7 Aug
Number of Census Days				
Incubation Period	8	1	0	0
Chick Period	6	4	7	2
T o t a l	14	5	7	2

[1] No murre chicks had left the cliffs when field crews left the study site on 25 August.

[2] One murre chick was seen on water on 7 August; none was seen again until 11 August, when many were on the water.

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TABLE 2, Summary of murre census results at Cape Thompson, 1960-1979.

A. Raw results, averaged between (among) observers counting simultaneously.

Year	Colony 1	2	3	4	5[a]	Total
1960	4,187 (100)[b]	76,249(100)	26,814(100)	B,726(100)	134,532(100)	250,508(100)
1961	4,589 (110)[c]	NC	NC	6,445(74)	NC	NC
1976	4,293 (103)[d]	46,722(61)	19,098(71)	6,894(79)	79,650(59)	156,657(62)
1977	2,471 (59)	52,320(69)	21,282(79)	7,621 (87)	58,995(44)	142,689(57)
1979	2,302 (55)[e]	50,034(66)	15,822(59)	6,157 (71)[d]	39,756 (30)[f]	114,071 (46)[f]
					45,161(34) [g]	119,476(48) [g]

NC: No census,

[a] In 1960 18 plots of Colony 5 were counted from above on land; in 1976 and 1977 those as well as all other plots were counted by observers in a boat. In 1979 nine of those 18 plots were counted from land and all others from a boat,

[b] Percent of 1960 count.

[c] Mean of 3 censuses.

[d] Mean of 2 censuses.

[e] Mean of 4 censuses.

[f] Boat-based counts only.

[g] land counts at 9 plots at Colony 5.

B. Results compensated for daily (1979 only) and diurnal (all years) variation in cliff attendance of murres.

Year	1	2	3	4	5[a]	Total
1960	4,200 (100)[b]	110,000(100)	39,000(100)	10,000(100)	194,000(100)	357,200(100)
1961	4,500(110)	NC	NC	8,900(89)	NC	NC
1976	2,100(50)	51,000(46)	24,000(62)	7,100(71)	115,000(59)	199,200(56)
1977	2,500(59)	55,113(50)	21,951(56)	8,053(81)	83,000(43)	171,000(48)
1979	2,382(57)	51,027(46)	25,447(64)	6,621(66)	63,242(32)	148,719(42)

NC: No census.

[a] Compensation was also made to correct for the discrepancy between land-based and boat-based counts (see text).

[b] Percent of 1960 total.

TABLE 3.   Summary of murre census results at Cape Lisburne.

A.   Raw results, averaged between observers counting simultaneously

	Raw Census Results			Date of First Hatching
Year	Subsample A[a]	Subsample B[b]	Total	
1976	9,925	14,100	129,575	6 August
1977	10,106	15,501	131,420	1 August
1978	9,524	NA	NA	21 July
1979	10,390	16,123	NA	22 July
1981	10,108[c]	14,236	NA	26 July

B.   Results compensated for daily (1981 only) and diurnal variation in cliff attendance.

	Compensated Census Results		
Year	Subsample A	Subsample B	Total
1976	NA	NA	NA
1977	14,779	22,138	184,000
1978	14,094	NA	NA
1979	17,342	26,050	NA
1981	11,968	17,735	NA

NA: Not available.

[a]   Plots 11, 12, 25, 26, 30, 32.

[b]   Subsample A and plots 65, 66, 70, 72.

[c]   Average of two censuses.

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TABLE 4. Dates of murre censuses in relation to breeding phenology at Bluff.

Event	1975	1976	1977	1978	1979	1980	1981
First Hatching[a]	NA	27 Jul	3 Aug	15 Jul	< 15 Jul	< 19 Jul	11 Jul
First Sea-going[a]	NA	~ 14 Aug	20 Aug	31 Jul	2 Aug	> 24 Jul	~ 29 Jul
Census Dates	(4 Jul)[b]	(26 Jun)	(26 Jun) (11 Jul)	(26 Jun)	20 Jul	21 Jul	15 Jul
	1 Aug	26 Jul	7 Jul	18 Jul	31 Jul	23 Jul	19 Jul
	(8 Sep)	12 Aug	29 Jul	9 Aug	7 Aug		
			19 Aug	(14 Aug)			

NA: Not available.

[a] If first dates of either hatching or sea-going were unknown, they were calculated assuming an interval of 18 days between hatching and sea-going (see Ramsdell and Drury 1979).

[b] Dates in parentheses are out of the range of the Census Period and results of censuses on those dates have not been included in the analyses.

TABLE 5. Murre numbers and reproductive success at Bluff, 1975-1981.

| Year | Census Results[a] | | | | Reproductive Output[b] | |
| | Census | | | | | |
	1	2	3	Average	k'[c]	k"[d]
1975	69,900	--	--	69,900(100)[c]	--	0.18
976	45,175	55,390	--	50,283(72)	~0.10[f]	0.04
977	39,250	36,100	--	37,675(54)	0.39	0.34
978	33,520	46,560	.-	40,040(57)	0.52	0.44
979	28,284	43,275	33,370	34,976(50)	0.53	0.50
1980	33,655	27,875	--	30,765(44)	0.62[g]	ND
1981	29,975	27,845	--	28,910(41)	-0.40[g]	ND

ND: No data, field crew left the colony before sea-going commenced.

[a]   Values reported here are the averages of observers' counts, if two or more observers counted murres during a particular census.

[b]   For values prior to 1979, see Drury et al. 1981, Ramsdell and Drury 1979 and Biderman et al. 1978.

[c]   Number of eggs hatching/average number of individuals on the Productivity Plots.

[d]   Number of sea-going chicks/average number of individuals on the Productivity Plots.

[e]   Percent of the 1975 count is listed in parentheses.

[f]   Calculated on the basis of average figures reported by Drury (1978).

[g]   When field crews left the colony, hatching was not yet complete.   This figure represents the midpoint between the minimum number known to hatch and the maximum number that could have hatched (number of eggs plus number still being incubated).

TABLE 6. Results of counts of murres at two study plots at Bluff, 1979-1981.

| | Location | |
Year	Stake 10	Stake 15
1979	$1,452 \pm 99(15)$[a]	$797 \pm 116(14)$
1980	$1,354 \pm 55(5)$	$841 \pm 39(4)$
1981	$1,446 \pm 73(11)$	$991 \pm 60(8)$
Pairwise Comparisons [b]	1979>1980<1981	(1979 = 1980) <1981

[a] Mean ± standard deviation (sample size). All counts were started at 1700 h (Bering Daylight Time).

[b] Alpha level = 0.05.

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TABLE 7.   Values of parameters used in the population model.

|	Parameter	Value	Source
A.	Adult Survivorship	0.915	Birkhead & Hudson (1977)
B.	Subadult Survivorship	0.339	See Text
	1. First-year	0.5545	See Text
	2. Second-year	0.80	See Text
	3. Third-year	0.85	See Text
	4. Fourth-year	0.90	See Text
C.	Reproductive Success (average predicted success, 1942-1980)	0.334	See Text
D.	Age at Maturity	5 years	Birkhead & Hudson (1977)
E.	Ratio of Breeding Pairs/Average Number of Individuals (k)	0.61	Present Study
F.	Proportion of Age Class using Breeding Ledges		Birkhead & Hudson (1977)
	1. One-year olds	0	Birkhead & Hudson (1977)
	2. Two-year olds	0	Birkhead & Hudson (1977)
	3. Three-year olds	0.50	Birkhead & Hudson (1977)
	4. Four-year olds	0.75	Birkhead & Hudson (1977)
	5. Adults	1.00	Birkhead & Hudson (1977)
G.	Proportion of Individuals at Ledges during Counts	0.75	See Text
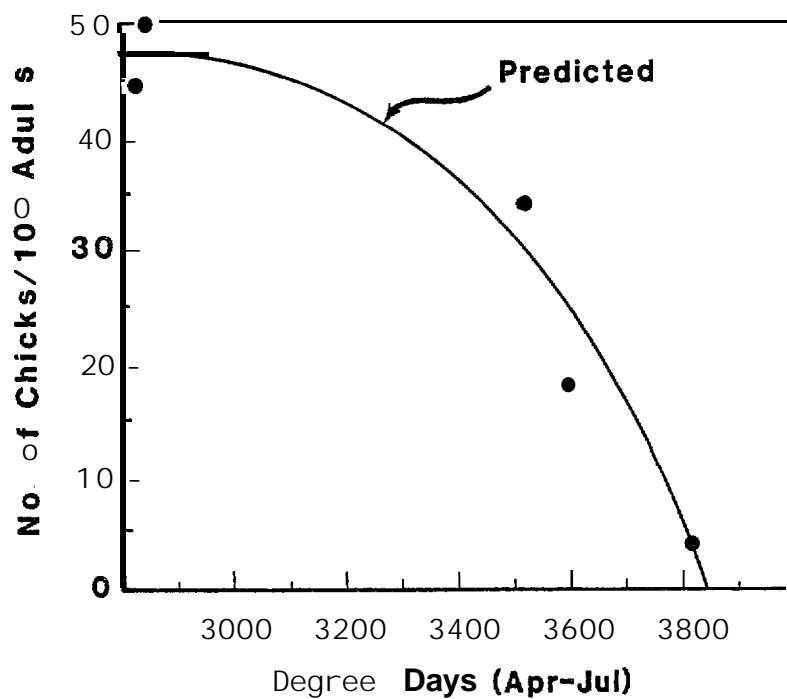
Figure 1. Relationship between reproductive success
(number of sea-going chicks/100 adults) at
Bluff, and cumulative heating degree days
in April-July at Nome. The equation of
the line is:

Number of chicks/100 adults = 4.62×10^1 +

2.36×10^{-2} (Degree days - 2800) -

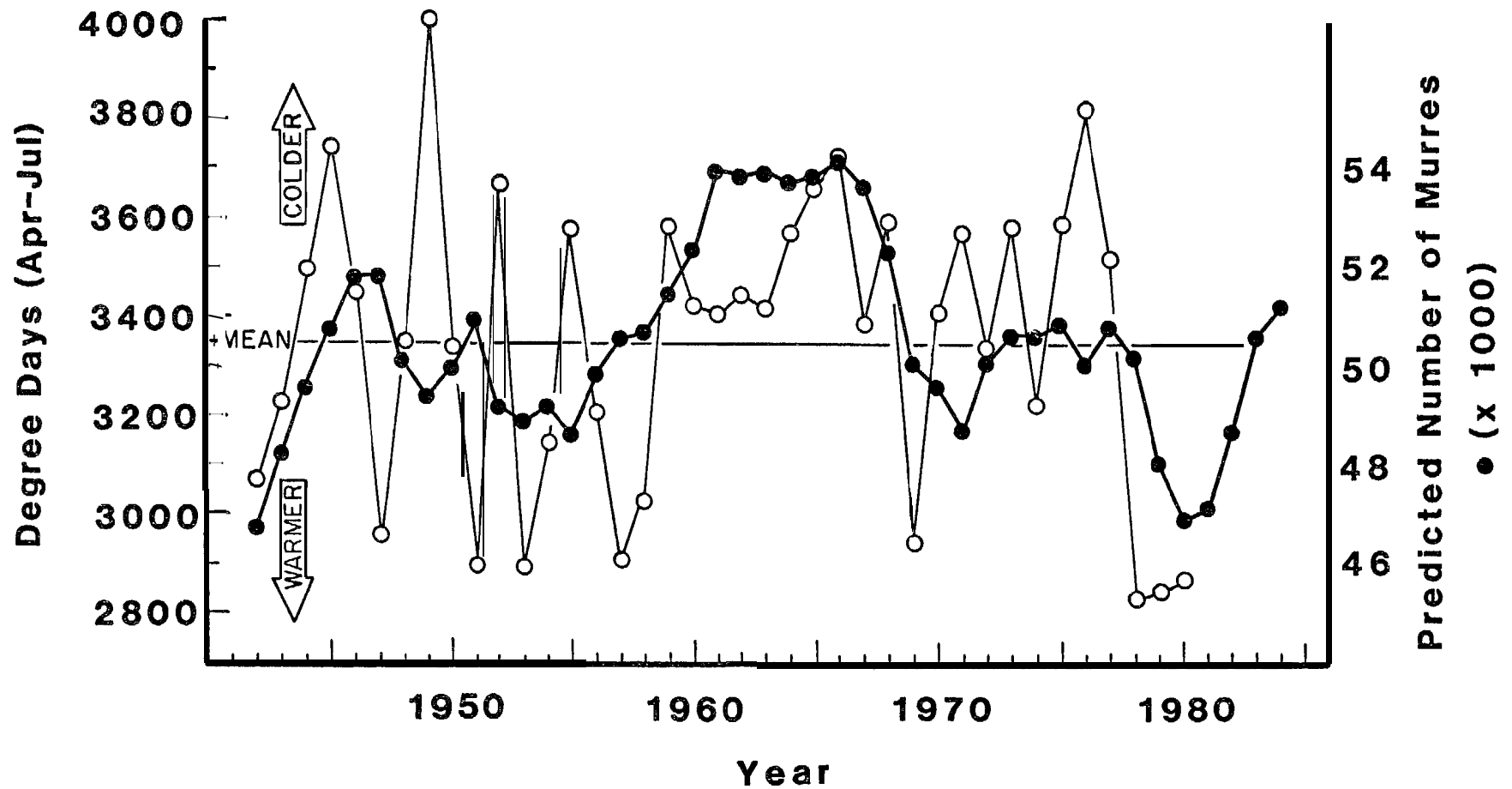6.55×10^{-5} (Degree days - 2800)^2.

Figure 2. Cumulative heating degree days in April–July at Nome (open circles), and the predicted number of murres at Bluff (closed circles). Based on data in Figure 1.
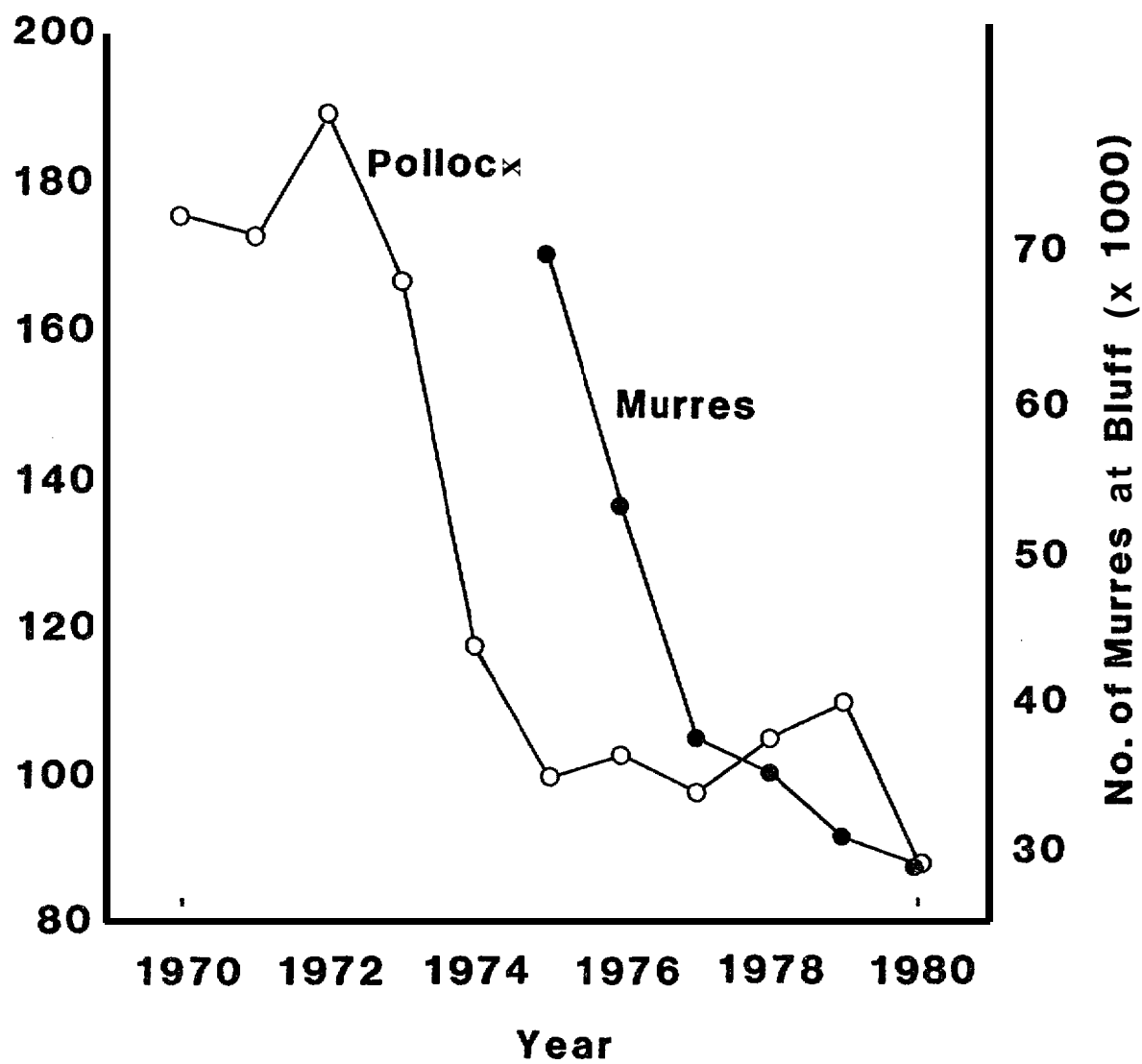
Figure 3. Catch per Unit Effort of pollock in the southeastern Bering Sea
(Bakkala *et al*. 1981), and numbers of murres at Bluff.

Field work was conducted during a portion of each summer of 1976-1979 at Cape Thompson and 1976-1981 at Cape Lisburne. In each year, except 1976 at Cape Lisburne, murres and kittiwakes were collected at intervals as they returned to the colonies from offshore feeding areas. Most birds fed at a considerable distance from the colonies at both sites (see Results), and it was not practical to visit these areas to collect specimens. A few birds were also collected as they fed near the colonies. Generally within two hours of collection the stomach contents and the lining of the proventriculus were removed and stored in 70% ethanol. Food items were later sorted and identified using appropriate taxonomic keys and preserved reference material.

Prey remains were usually in an advanced stage of digestion by the time the birds returned to the colonies. Invertebrate prey items were often identified by parts such as rostra, jaws, uropoda and eyes. Fishes were identified from otoliths. Sculpins (Cottidae) were also counted and identified on the basis of preopercular bones. The following data, therefore, are probably biased towards hard-bodied prey, and especially towards fishes since otoliths appear to persist in digestive tracts longer than other types of prey remains. A recent discussion of such problems associated with food habits studies of thick-billed murres has been presented by Bradstreet (1980).

The sizes of most fish prey were reconstructed from regressions of fish length on otolith length, and from fish weight on fish length. The equations used are presented in Table 1. Sculpins were often not identifiable to species or genera, and for the purposes of this analysis all were considered to be *Myoxocephalus quadricornis*. *M. quadricornis* was a common species in the region (Alverson and Wilimovsky 1966, Craig and Haldorson 1981), one that occurred regularly in prey remains, and the only species of sculpin in the eastern Chukchi for which size data were available. Two other sculpins were also frequently encountered, *Icelus sp.* and *Artediellus sp.* Righteye flounders (Pleuronectidae) were generally young-of-year fish and were assigned an average weight of 1.0 g. "Other fishes" (see Results) were a variety of taxa including snailfishes (Cyclopteridae, especially *Liparis sp.*), pricklebacks (Stichaeidae, especially *Stichaeus punctatus* and *Chirolophus sp.*), and herring *(Clupea harengus)*. They occurred in several sizes but were generally small and were assigned an average weight of 2.0 g.

Intact invertebrates were measured and average weights were used to reconstruct wet weights of certain groups. Average weights of amphipods (Amphipoda) and mysids *(Neomysis sp.* and *Mysis sp.)* were about 0.2 g, euphausiids *(Thysanoessa sp.)* about 0.1 g, and shrimp (predominantly *Pandalus sp.* and *Eualus sp.)* about *0.5 g.* Polychaetes *(Nereis sp.)* were assigned an average weight of *1.0 g* and "Other invertebrates (see Results), including hermit crabs *(Labidochirus splendescens),* squids (Cephalopoda) and snails (Gastropoda) were assigned an average weight of *0.5 g.*

Most information on feeding areas used by murres and kittiwakes at Cape Thompson and Cape Lisburne was obtained annually by land-based observations of directions taken by birds as they flew to and from the colonies., and by similar boat-based observations along the coastline up to 60 km from the colonies. In 1978 a Cessna 336 aircraft was used to complement the land and boat-based observations during 25-29 July and 18-19 August . Transects were flown up to 130 km from the colonies at about 45 m above the water and at ground speeds of about 190 km hr.$^{-1}$ Observations were made from both sides of the aircraft by two or three observers. Numbers of birds on the water were summed during five minute intervals and numbers of birds in the air and their flight directions were recorded. The positions of the transects were determined from time and heading information and from radar fixes provided by U.S. Air Force stations at Cape Lisburne and Point Lay.

VIb. FOOD HABITS - RESULTS

Food Habits

Food habits of murres and kittiwakes during all years combined (Tables 2 & 3) were similar at the two colonies. A notable difference was the absence of mysids and euphausiids at Cape Thompson. Dietary differences among the three species were similar to those reported previously for Cape Thompson (Swartz 1966) and for the Pribilof Islands (Hunt *et al.* 1981). Thick-billed murres demonstrated the greatest diversity in food habits and common murres the least. Both species of murres fed on similar kinds of fishes, although common murres took many fewer sculpins and "Other fishes". Common murres also fed on very few invertebrates. Kittiwakes rarely fed on sculpins and never on flatfishes, benthic taxa that would generally not be available to kittiwakes because of the kittiwakes' restricted feeding depth. Polychaetes were taken relatively more frequently by kittiwakes than by murres at both colonies, as were euphausiids at Cape Lisburne. The apparently large contribution of amphipods to diets of kittiwakes at Cape Lisburne is misleading since all but one were recovered from a single bird.

Annual differences in the overall importance of fishes and invertebrates to thick-billed murres and kittiwakes were seen at both colonies (Table 4, Figure 1). Proportionally fewer fishes were recovered from birds in 1976, with steadily increasing relative importance in succeeding years. As suggested by data in Table 5, annual increases in fish biomass were primarily responsible for annual differences in the relative utilization of fishes and invertebrates.

Seasonal patterns were also apparent in the use of fishes and invertebrates by thick-billed murres, but the patterns were not the same at the two colonies (Table 4). The greatest proportional use of invertebrates occurred early in the summer at both colonies, with fishes assuming greater importance later in the breeding season. A regular progression of increasing dominance by fishes occurred at Cape Lisburne, while the highest proportion of fishes at Cape Thompson was taken during the interval 1-20 July in two of the three years for which the data are complete.

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A seasonal pattern similar to that at Cape Thompson was reported for the Pribilof Islands by Hunt *et al.* (1981), where the importance of invertebrates in the diets of thick-billed murres was highest in June and lowest in July.

The importance of various fish taxa to murres and kittiwakes changed seasonally (Tables 6 & 7). Cods (Arctic cod, *Boreogadus saida* and saffron cod, *Eleginus gracilis*) were most common in the birds' diets early in the season and declined steadily in importance as sand lance *(Ammodytes hexapterus)* rose in importance throughout the summer. Seasonal patterns of importance of invertebrate taxa were less conspicuous and less consistent (Table 8), except that polychaetes were most common early in summer. This trend was most pronounced in kittiwakes; all of the polychaetes taken by kittiwakes at Cape Lisburne and 99% of those taken at Cape Thompson were taken during the interval 1-20 July. Polychaetes spawn in the water column in early summer (H. Feder pers. comm.), and the heteronereid worms become available to murres and kittiwakes at that time.

Seasonal and annual differences in utilization of various fish taxa by murres and kittiwakes are accentuated if the taxa are grouped as in Figure 2 and Table 9. The trend is for the combined importance of sand lance and capelin *(Mallotus villosus)* to be greater later in the season of all years, except in 1979 at Cape Thompson, and to be greater earlier in the season each year after 1976. Hunt *et al.* (1981) also reported that numbers of sand lance increased in diets of black-legged kittiwakes on the Pribilofs from early through late summer.

Characteristics of Prey Populations

Size distributions of principal taxa of prey fishes are shown in Figures *3-13*. Included for comparison are data we collected in 1978 and 1980 at Bluff, a seabird colony in Norton Sound (northeastern Bering Sea), and that L. G. Swartz (unpubl. data) collected at Cape Thompson in 1960.

The average size of sand lance recovered from murres and kittiwakes was significantly larger each successive year between 1977-1980 at all three colonies (ANOVA, P < 0.05). Age determinations, based on opaque and hyaline zones of otoliths (see Reay 1972), indicated that the majority of the sand lance were age class 1+, with fewer age class 0+ individuals. Sand lance older than age class 1+ were infrequent, except at Cape Lisburne in 1977 when age class 2+ fish were common and accounted for the unusual bimodal size distribution that year. Andriyashev (1954) noted that sand lance in the coastal zone of Murmansk also were predominantly age class 1+, and Hatch *et al.* (1979) reported that all of the sand lance fed to tufted puffin *(Lunda cirrhata)* and rhinoceros auklet *(Cerohinca monocerata)* chicks on Middleton Island (northern Gulf of Alaska] were age class O and 1.

Capelin were significantly larger in 1979 than in 1977 at Cape Thompson and were significantly larger in 1980 than in 1979 at Cape Lisburne (ANOVA, P < 0.05). Capelin were not aged, but they were predominantly age class 1+ according to age-length distributions of capelin from . the Grand 'Bank reported by Pitt (1958 a).

The same trend of increasing average size in later years was also seen in Arctic cod, and differences between 1977-1978 and 1978-1979 at Cape Lisburne were significant (Kruskal-Wallis test, P < 0.05). The size distributions of Arctic cod tended to be bimodal; smaller fish were predominantly age class 1 and the larger fish were age class 3 (see Table 10). The annual increases in average size of Arctic cod at Cape Lisburne resulted from changes in relative numbers of the two age classes between years, as well as from apparent annual increases in average sizes of age class 1 fish. Craig and Haldorson (1981) reported that the sizes of age class as 1-5 Arctic cod in Simpson Lagoon (northeast of Cape Lisburne in the Beaufort Sea) were larger in 1978 than in 1977, and the difference was significant for age class 2 fish, which averaged 15 mm larger in 1978 (t=3.6, P <0.001). At Cape Thompson the average size of Arctic cod decreased between 1976 and 1977 because of a large change in proportions of age classes 1 and 3 fish. However, it appears that the average sizes of individual age classes may have increased between years, especially between 1977 and 1979, as it did at Cape Lisburne and Simpson Lagoon.

Differences between years in sizes of sculpins are even more difficult to interpret because the "population" each year consisted of various numbers of at least three species. The majority of sculpins in all years were apparently age classes 0-2 (see Table 11). Nevertheless, the average length of sculpins increased between most years at both Cape Thompson and Cape Lisburne. The increases were significant between 1976 and 1977 at Cape Thompson, and between 1978-1979 and 1979-1980 at Cape Lisburne (Kruskal-Wallis test, p < 0.05).

Saffron cod were considerably smaller than Arctic cod, and most were apparently age class 0 fish with perhaps a few age class 1 fish (see Table 12). Unlike Arctic cod, sand lance, capelin and sculpins, saffron cod were smaller in successive years, except between 1978-1979 at Cape Thompson, and the differences were all significant (Kruskal-Wallis test, p < (),()5). Conversely, saffron cod were much larger in 1980 than in 1978 in Norton Sound, although the difference in that region was apparently the result of age class changes between years rather than changes in size at age. A change in age class strength might also explain the difference in size of saffron cod between 1978 and 1979 at Cape Thompson.

Sand lance, capelin, sculpins and Arctic cod also exhibited a trend towards increasing size with decreasing latitude. Within all years that samples were collected at both Cape Thompson and Cape Lisburne, sculpins and capelin were always significantly larger at Cape Thompson. Sand lance were larger at Cape Thompson than at Cape Lisburne in 1978 and 1979 and the difference was significant in 1979. In 1977 sand lance were significantly larger at Cape Lisburne because of the unusually high occurrence of age class 2+ fish. Sand lance at Bluff were significantly larger in 1978 than at the other two colonies that year, and in 1980 they were significantly larger than any of the other samples we obtained. Arctic cod were larger at Cape Thompson than at Cape Lisburne in 1977 and 1979 and the difference was significant in 1977. Increasing fish size with decreasing latitude has also been reported by Andriyashev (1954) for sand lance in the Barents Sea, and by Lowry and Frost (1981), who showed that Arctic cod in the Bering Sea were larger than in the Chukchi and Beaufort Seas.

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Size distributions of principal species of invertebrates recovered
from murres and kittiwakes at Cape Thompson and Cape Lisburne are presen-
ted in Figures 14-17. *Parathemisto libellula* were significantly larger
at Cape Lisburne in 1977 than in 1978, or than at Cape Thompson in 1979
(ANOVA, P < 0.05). Similarly, euphausiids *(Thysanoessa sp.)* were signif-
icantly larger at Cape Lisburne in 1978 and 1979 than in 1980 (ANOVA,
p < 0.05). However, all of the individuals measured in 1978 and 65% of
those measured in 1979 were taken from thick-billed murres, compared to
only 2% in 1980. In 1979, thick-billed murres took significantly larger
individuals than did kittiwakes (Figure 18), a fact that could account
for the apparent size difference of euphausiids in 1980.

Feeding Areas

Although Cape Thompson and Cape Lisburne are separated by only about
85 km, feeding areas of seabirds from these two colonies were much farther
apart during most of each summer. Generally, birds from Cape Thompson fed
to the south of the colony during June and July, and shifted more to the
west and north in August. Birds from Cape Lisburne fed to the northeast
in Ledyard Bay during June and July, and shifted more to the north in
August . Only during August of some years was there ever any overlap in
foraging areas of birds from the two colonies.

Figure 19 illustrates the combined land and aerial observations we
made on feeding areas of murres during this study. Most of the murres
from Cape Thompson fed south of the colony in all years during June and
most of July. In 1976 murres shifted more to the west in August, but few
were ever seen commuting north. A clear shift to the north occurred in
late July of 1977 and by early August nearly all murres from Cape Thomp-
son fed north of the colony. Although a similar shift happened in 1978,
there was less distinction between early and late season feeding areas.
Many murres continued to feed south and west of the colony after many
others had begun feeding to the north and northwest. In 1979 murres fed
over an even broader area throughout the summer than during the previous
year. Flight directions were already widely scattered between south and
west in early July. About half of the murres shifted to the west and
north by early August, and thereafter murres could be seen flying to and
from nearly all offshore directions.

These observations of feeding areas of murres from Cape Thompson are
supported by both shipboard and aerial surveys made in earlier years.
Swartz (1967), reporting on shipboard transects made in the eastern
Chukchi Sea during August 1960, stated that the principal feeding area of
murres from Cape Thompson appeared to lie between 25-65 km south of the
colony. Fewer murres were seen to the west. Harrison (1977) reported
seeing concentrations of murres approximately 70 km south of Cape Thomp-
son during aerial surveys flown in June 1975. He also reported fewer,
but substantial, numbers of murres in the same region in August 1976.
Concentrations of murres were also seen in the same general area by ship-
board observers in early September 1976 (Gould 1977).

Very few murres were ever seen on the water between Cape Thompson
and Cape Lisburne, except in the immediate vicinity of the colony at

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Cape Lewis, during any of our aerial surveys or during numerous flights between the colonies at other times. When Cape Thompson murres fed north of the colony, therefore, they probably went to the same area used by birds from Cape Lisburne. In August of 1978 we intercepted several flocks of southbound murres west of Cape Lisburne and followed them to Point Hope in our survey aircraft. At Point Hope we watched other flocks arriving from the same direction and subsequently confirmed that these flocks were returning to Cape Thompson.

Other observations of murres flying south past Point Hope during the summer have been made in the past. R. M. Gilmore (unpubl. field notes) recorded watching "...endless flocks of Pallas murres fly by" as he sat at Point Hope on 4 August 1931. His conclusion was that the birds were on their southward migration because their directional orientation was from north to south. We believe that he was probably seeing flocks returning to Cape Thompson after feeding in the vicinity of Cape Lisburne. Nelson (1969) also reported that during summer murres "... constantly fly north or south over Point Hope spit.. ." . Although he believed that the birds were flying back and forth between the colonies at Cape Thompson and Cape Lisburne, and mentioned wind as a causative factor determining northward or southward flight directions, we suggest that he too was seeing murres departing from Cape Thompson and returning there after feeding well north of Cape Lisburne.

Murres at Cape Lisburne fed to the northeast of the colony in Ledyard Bay during June and July of all years. By early August of each year they shifted their foraging effort more to the north. By late August most Cape Lisburne murres foraged to the north and northwest of the colony. The aerial transects flown in late July 1978 showed that murres were feeding in a relatively well-defined region east of a line between Cape Lisburne and Point Lay. By mid-August 1978, aerial surveys found the majority of murres concentrated north of the colony, with fewer to the west and east.

Although the pattern of seasonal feeding area use was less variable at Cape Lisburne than at Cape Thompson, some differences between years have occurred. In early September 1976 the majority of murres fed more to the northwest and west than in following years. Swartz (1967) also reported relatively large numbers of murres westward of the colony in late August 1960.

Kittiwake feeding areas tended to be closer to the colonies, but generally lay in the same direction as those of murres in June and July. Beginning in late July or early August of all years except 1976, kitti- wakes concentrated along the coastline north and south of Cape Thompson and east of Cape Lisburne. The shift to coastal feeding occurred when sand lance and capelin appeared near shore east of Cape Lisburne and north of Cape Thompson. As shoals of these fishes moved west along the coast to Cape Lisburne and south to Cape Thompson, feeding intensified in front of both colonies. At Cape Thompson shoals of sand lance traveled well southeast of the colony and feeding effort shifted as far south as Kivalina in some years. When sand lance and capelin were absent in 1976, kittiwakes foraged widely offshore throughout the summer.

The large annual differences in abundance and size of forage fishes in the eastern Chukchi Sea indicate that there was substantial environmental variability in this region between 1976-1980. Sea ice and seawater temperature, very important elements of the highly seasonal environment of northern Alaska, fluctuated considerably during the past decade, and might have been responsible for many of the interannual and seasonal changes in seabird food webs, and hence in seabird breeding success, that occurred during that time.

The southern extent of ice in the Bering Sea has varied considerably between years, a consequence of changing weather patterns (Walsh and Johnson 1979, Johnson 1980, Niebauer 1980, 1981a, 1981b). Beginning in 1973, anomalous atmospheric circulation resulted in progressive cooling of the Bering Sea, which led to large negative deviations from normal sea-surface temperature and shelf bottom water temperature, and a large positive deviation from normal ice cover by 1976 (Dickson and Namias 1979, Niebauer 1980). Between fall 1976 and spring 1979, however, the trend reversed; sea-surface temperature, which was 1.4°C below normal in 1975, rose $0.7 - 0.8°C \ yr^{-1}$, and sea ice, which had reached its maximum southern extent in the winter of 1975-76, decreased about 10% yr^{-1} from 1977 through 1979 (Dickson and Namias 1979, Niebauer 1980). Annual changes in ice cover and sea-surface temperatures were not confined to the Bering Sea, but were equally pronounced in the eastern Chukchi Sea as shown in Figure 20.

Besides sea ice, the eastern Chukchi Sea is dominated by a strong barotropic current flowing north out of the Bering Sea (Coachman et al. 1975, Coachman and Aagaard 1981). Water velocity of 150 cm sec^{-1} through Bering Strait is common and mean transport is in the order of $1 - 2 \times 10^6 \ m^3$ see-1. A major component of the flow is Alaska Coastal Water, a well defined warm water mass of low salinity found on the eastern side of the strait. North of Bering Strait, Alaska Coastal Water tends to follow the 40 m contour interval which takes it eastward toward the Cape Thompson-Point Hope region. North of Point Hope the current splits with part flowing northwest into the central Chukchi Sea and part flowing northeast around Cape Lisburne and into the Beaufort Sea east of Barrow (Flemming and Heggarty 1966, Hufford 1973, Coachman et al. 1975).

Alaska Coastal Water develops annually in the northeastern Bering Sea from cold, relatively saline water remaining from winter that is diluted by melting ice and river input, primarily from the Yukon River, and rapidly heated by insolation (Coachman et al. 1975). The temperature of coastal water flowing through Bering Strait may rise from near 0°C to 10°C during the first month following dissipation of sea ice (Bloom 1964, Ingraham 1981). Therefore, the seasonal development of the Alaska Coastal Water mass depends on the winter extent of ice into the Bering Sea, its rate of retreat in spring and the spring temperature of Bering Sea parent water.

The relationship of Alaska Coastal Water to the marine biology of the eastern Chukchi Sea is not well known, but it may have a major direct effect by ameliorating an otherwise colder arctic environment (Flemming and Heggarty 1966). It may have other important effects by 1) advecting into the region particulate organic matter that subsidizes local primary production and helps feed endemic zooplankton and benthic invertebrate populations, and by 2) advecting in oceanic and neritic zooplankton stocks' originating in the Bering Sea, but constituting an important food source for eastern Chukchi fish populations.

The Bering Sea shelf shoreward of about 100 m has relatively high levels of primary productivity, in the order of 3 g C m^2 day^{-1} (Cooney and Coyle MS). Poor coupling to pelagic herbivores, however, results in a relatively inefficient system, with a major fraction of the annual primary production being lost to endemic pelagic food webs. The turbulent Bering Strait region also has high levels of primary productivity, comparable to upwelling areas off of the west coasts of North and South America and Africa (McRoy *et al.* 1972, McRoy and Goering 1976). Because of the volume and speed of water transported through the strait, a significant portion of the carbon fixed there during summer is probably swept downstream. Stoker (1981) suggested that such a process would explain high standing stocks of predominantly boreal Pacific benthic invertebrate macrofauna in the southern Chukchi Sea, Particulate organic matter advected off of the northern Bering Sea shelf, plus that originating in Bering Strait, could therefore be expected to contribute significantly to the annual carbon budget of the eastern Chukchi Sea.

The flow of water from the Bering Sea has also been shown to play an important role in determining the composition and abundance of zooplankton assemblages in Bering Strait and the eastern Chukchi Sea. A variety of endemic Bering Sea copepods, including *Eucalanus bungii, Calanus cristatus, C. plumchrus, Acartia longiremis* and *A. clausi,* are advected into the eastern Chukchi Sea during summer, and contribute significantly to diversity and standing stocks of zooplankton in the near shore waters (Johnson 1956, Redburn 1972, Cooney 1981). The intrusion of warm water also creates a temperature regime favorable for the rapid development and high production of meroplankton, particularly barnacle larvae, and as a result, zooplankton biomass in the warmer coastal zone during summer is about an order of magnitude higher than in the colder central Arctic Ocean (Redburn 1972).

Little is known about the natural histories of the various fish populations that are important to seabirds in the eastern Chukchi Sea. Information obtained elsewhere on any of the same or similar species, however, indicates that distributions and numbers of populations of prey fishes could be influenced by the effects that Alaska Coastal Water has on regional water temperatures an? on zooplankton standing stocks.

Sand lance are generally considered a coastal, shallow water species except in winter when they move into relatively deeper water of 100-120 m (Macy *et al.* 1978). They spawn during a, long interval between fall and spring (Andriyashev 1954, Macy *et al.* 1978, Rogers *et al.* 1981). Beginning in mid-June in the Barents Sea, shoaling sand lance composed mainly

of year class 1+ fish run towards shore where they remain until August-October (Andriyashev 1954). We observed similar behavior of sand lance at both Cape Thompson and Cape Lisburne. For example in 1977, small numbers of sand lance were available to murres and kittiwakes in early July . These were at best, however, an insignificant vangard of shoals that were present after 25-30 July at Cape Lisburne, and after 10-12 August at Cape Thompson. Shoaling sand lance moved along the coast throughout the remainder of the summer at both colonies.

Several studies have shown that sand lance are sensitive to water temperature. Inoue *et* al. (1967) showed that sand lance eggs artificially incubated at 6°C took 33 days to hatch, whereas eggs incubated at 16°c hatched in only 13 days. Winslade (1974) reported that the emergence of sand lance *(A. marinus)* from sand where they overwintered was determined by warming water temperatures in spring. Sand lance *(A. dubious)* from the Grand Bank in the northwest Atlantic Ocean had slower first-year growth rates in colder years than in warmer years (Winters 1981).

Since sand lance spawn during winter, it might he assumed that the onshore runs in summer occur in response to seasonally abundant food. Sand lance are often found near the bottom where they apparently bury in the sand to avoid predators (Macy *et al.* 1978), but benthic organisms contribute little to their diets. Sand lance in the Barents Sea fed primarily on pelagic taxa such as *Calanus finmarchicus* and meroplanktonic forms of barnacles and larvae of euphausiids and amphipods during early summer, and shifted to small copepods, particularly *Microsetella, Acartia* and *Oithona*, towards late summer (Andriyashev 1954). Sand lance in the northern Gulf of Alaska fed predominantly on calanoid copepods and barnacle larvae (Blackburn *et* al. 1981, Rogers *et* al. 1979). Sand lance taken by seabirds in the eastern Chukchi Sea during this study fed on large numbers of small calanoid copepods *(cf.* C. *plumchrus)*.

Changes in the physical environment (i.e. the extent and duration of sea ice and the development of the Alaska Coastal Water mass) of the magnitude seen in the Bering Sea and eastern Chukchi Sea during the 1970's could reasonably be expected to have led to the changes we observed in the sand lance population between 1976-1980. Smaller sizes of sand lance in colder years could have resulted from water temperature alone, by its effects on metabolism and growth for example, or could have resulted from poor coupling to seasonally abundant prey because of prolonged incubation time of eggs, delayed emergence of larvae and adults in spring, and delayed development of zooplankton populations. The annual changes in seasonal abundance of sand lance also could have been a function of differential rates of development of neritic prey populations or of delayed emergence times of overwintering fish.

Most of the capelin eaten by murres and kittiwakes were age class 1+ juveniles, although remains of a few larger adults were also recovered. The adults were spawning *as* evidenced by developing reproductive products in both sexes. Adult capelin do not feed while spawning, but juveniles feed intensively throughout the summer, predominantly on copepods (Vesin et al. 1981). The presence of juvenile capelin near Cape Thompson and

Cape Lisburne in summer could be a response to seasonally abundant food, as in the case of sand lance.

Pitt (1958b) reported that capelin on the Grand Bank will spawn in a rather broad range of water temperatures, but spawning and embryonic development is delayed in colder years. In 1950, relatively cold water temperatures resulted in spawning in mid-July, and larvae were liberated in late September. In 1951 when water temperatures were about 2°C warmer, spawning occurred in late June-early July and larvae were liberated around the first of August. Pitt (1958a) also showed that growth rates of capelin were slower in colder years than in warmer years, and suggested that the difference was a factor of water temperature and food conditions. Annual differences in seasonal warming patterns in the eastern Chukchi could easily account for the annual differences in the sizes of capelin in 1977-1980.

By far the most abundant and widespread fish fauna in the eastern Chukchi Sea are Arctic cod and sculpins (Alverson and Wilimovsky 1966, Craig and Haldorson 1981). Arctic cod feed on typically arctic copepods, amphipods and mysids (Lowry and Frost 1981, Craig and Haldorson 1981). Sculpins feed mainly on mysids, amphipods and isopods (Craig and Haldorson 1981). The degree to which these Arctic food webs might be subsidized by carbon imported from the Bering Sea is unknown. If there is a positive effect, then it should be larger in warmer years when the annual production cycle begins relatively early in summer, and it should be greatest just north of Bering Strait where the suspended particulate load would be highest. Increasing sizes of Arctic cod and sculpins between 1976-1980, and from north to south, would suggest such effects.

Cod and sculpin populations might also benefit if their prey concentrated along the front separating Alaska Coastal Water from the adjacent water mass in the eastern Chukchi Sea. A rather sharp boundary exists in summer between these two water masses (Coachman *et* al. 1975), similar to fronts separating water masses in the southeastern Bering Sea (Coachman and Charnell 1979, Shumacher *et* al. 1979). During our aerial surveys in 1978, the number of murres on the water declined sharply after we crossed a frontal line running northeast-southwest across the mouth of Ledyard Bay between Cape Lisburne and Point Lay. Kinder *et* al. (MS) have recently described a similar relationship in the southeastern Bering Sea. They found murres concentrated near a front that surrounds the Pribilof Islands in summer, and suggested that these aggregations were related to the availability of walleye pollock *(Theragra chalcograma)* that were feeding on zooplankton concentrated along the front. Annual differences in the development of Alaska Coastal Water and the associated front separating it from the adjacent water mass in the central and northern Chukchi Sea could thereby lead to annual differences in energy flow through food webs that include Arctic cod and sculpins.

Annual and seasonal differences in murre feeding areas also indicated that arctic benthic and demersal food webs, as well as neritic food webs, might benefit from energy exported from the Bering Sea. In June and July of all years, murres at Cape Thompson fed to the south, toward the source of the flow where energy levels should be highest relatively early in the season. As summer progresses in this region, zooplankton,

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for example copepods that are plentiful in the water column as eggs, nauplii and copepodids in early summer, may decline in numbers as the larval forms mature and migrate to deeper water where they overwinter. The shift in murre flight directions from south to west to north at Cape Thompson might indicate that the birds followed the movement of a pass- ively mobile assemblage of organisms advected north before the annual production cycle began to shut down in the northern Bering-Bering Strait region. Similarly, the shift in murre flight directions from northeast to north and northwest at Cape Lisburne suggests that those birds also responded to this drifting assemblage of organisms as it passed their colony. By mid-August of several years, the center of murre prey biomass appeared to be situated north and west of Cape Lisburne, because at that time the majority of the birds from Cape Lisburne and large numbers of murres from Cape Thompson fed there. Indeed, Wing (1974) showed that copepod biomass and diversity were greatest in a region of relatively warm water northwest of Cape Lisburne in September-October 1970. The occurrence of a variety of fish species was also higher there at that time than in surrounding waters (Ingham et al. 1972). Annual variations in foraging patterns of murres at Cape Thompson might be explained by the way a drifting, maturing food web could be affected by differences in timing of the annual production cycle in the Bering Sea.

The changes we observed in the breeding biology of murres and kitti- wakes between 1976-1979 and the corresponding changes in prey populations probably represented adjustments to the large-scale environmental fluctu- ation that occurred during that time. Although we lack many of the details, the effects of climatic changes during the 1970's were apparently manifested in two very different food webs, arctic benthic and demersal food webs that include cods and sculpins, and boreal neritic food webs that include sand lance. Furthermore, environmental effects on seabirds and their food webs were not restricted to Cape Thompson and Cape Lisburne. Drury et al. (1981) andwe documented the same pattern of breeding failure followed by recovery in kittiwakes and common murres in Norton Sound between 1975-1981. Figure 21 compares the relationships between environment and productivity for kittiwakes at Bluff and Cape Lisburne. Food availability at Bluff also seemed to be the most important factor in determining annual levels of reproductive success. Apparent food shortages likewise led to a poor breeding season for murres and kittiwakes on St. Lawrence Island (northern Bering Sea) in 1976 (Searing 1977). Murres and kittiwakes in Norton Sound feed primarily on sand lance and saffron cod, and on St. Lawrence Island they feed on cods, sand lance and capelin (Springer etal. unpubl. data). St. Lawrence Island and Norton Sound are located in the headwaters of the marine river that flows out of the Bering Sea and into the eastern Chukchi Sea. Breeding seabirds throughout the northern Bering-eastern Chukchi region may be related by common food web dependencies that are influenced by similar physical processes.

If energy flow through food webs in northern Alaskan waters waxes and wanes in response to patterns of environmental change during inter- vals of a few years, as it apparently did in the 1970's, it might also adjust to longer-term fluctuations in the environment (see Cushing and Dickson 1976). For example, between the late 1940's and mid-1960's,

sea-surface temperature over the bulk of the northern Pacific Ocean (15°
to 60° N and 130° E to 110° W) was generally normal or above; only about
three years in the mid-1950's were slightly below normal (Namias and
Cayan 1981). Since 1964, however, sea-surface temperature was above
normal in only three years. Such differences may alter energy budgets
in northern Alaska sufficiently to account for the declines in numbers
of murres that we have documented at Bluff and at Cape Thompson (Table
13). Below average temperatures in Norton Sound for many years could
have resulted in relatively less energy available to murres, relatively
low levels of natality, and the recent numerical decline as recruitment
fell below adult survivorship (see sections V.a - VII. a.). At Cape
Thompson, murre numbers were highest in 1960, a time when water tempera-
tures had been above normal for several preceding years. However,
relatively cold temperatures prevailed from the mid-1960's until we
resumed work there in 1976. A preliminary simulation analysis predicts
that at Bluff, murre numbers will increase beginning in 1982 as a conse-
quence of improved reproductive success associated with the warming trend
since 1978, if the population decline resulted from climatic fluctuation
and not other causes.

TABLE 1.   Regression equations used to estimate lengths and weights of principal fishes identified in prey remains of murres and kittiwakes collected in the eastern Chukchi Sea.

Fish	Equation	Sample Size	Correlation Coefficient	Source
Arctic cod (*Boreogadus saida*)	fish length (cm) = 2.198 x otolith length (mm) + 1.588	202	0.981	Frost and Lowry 1981
	log weight (g) = -5.196 + 3.o31 log length (mm)	277	0.98	Craig and Haldorson 1981
Saffron cod (*Eleginus gracilis*)	otoliths > 8.5 mm fish length (cm) = 2.323 x otolith length (mm) - 4.839	110	0.963	Frost and Lowry 1981
	otoliths ≤ 8.5 mm fish length (cm) = 1.740 x otolith length (mm)	36	0.932	Frost and Lowry 1981
	log weight (g) = -5.610 + 3.233 log length (mm)	180	0.94	Craig and Haldorson 1981
Sculpins[1] (Cottidae)	fish length (cm) = 4.009 x otolith length (mm) - 4.364			Frost and Lowry unpubl. data
	log weight (g) = -6.016 + 3.46 log length (mm)	272	0.98	Craig and Haldorson 1981
Sand lance[2] (*Ammodytes hexapterus*)	fish length (mm) = 4.01 x otolith length (units)[3] + 19.0	31	0.91	This study
Capelin[4] (*Mallotus villosus*)	fish length (mm) = 3.42 x otolith length (units)[3] + 29.22	12	0.99	This study

[1]Equations are derived from specimens of *Myoxocephalus quadricornis*.

Weights are approximated as: mean weight all fish = 2.0 g, Cape Thompson 1977; = 3.0 g, Cape Thompson 1978 and Cape Lisburne 1977-78; 4.0 g, Cape Thompson 1979 and Cape Lisburne 1980.

[3]12.5 units mm.[1]

[4]Heights are approximated as: mean weight all fish = 2.0 g, Cape Thompson 1977 and Cape Lisburne 1979; = 3.0 g, Cape Thompson 1979 and Cape Lisburne 1980.

TABLE 2. Importance of major taxa in diets of **thick-billed murres (TBM)**, common **murres** (CM) and black-legged kittiwakes **(BLK) collected** at Cape Thompson, eastern **Chukchi** Sea, 1976-1979.

	TBM n	TBM %[1]	CM n	CM %[1]	BLK n	BLK %[1]
Number examined	246	(100)	62	(100)	116	(100)
Number empty	33	(13)	13	(21)	11	(9)
Frequency of invertebrates	115	54	6	12	20	19
Frequency of fish	182	85	45	92	91	87

a. *Frequency of Occurrence*

	TBM n	TBM %[1]	CM n	CM %[1]	BLK n	BLK %[1]
Cods	85	40	29	59	55	52
Sculpins	87	41	14	29	0	0
Sand lance	45	21	20	41	32	30
Capelin	26	12	12	24	17	16
Righteye flounders	19	9	3	6	0	0
Other fishes	28	13	3	6	3	3
Shrimps	69	32	3	6	4	a
Amphipods	29	14	3	6	0	0
Mysids	0	0	0	0	1	1
Euphausiids	1	<1	0	o	0	0
Polychaetes	18	8	0	0	12	11
Other invertebrates	36	17	1	2	7	7

b. *Numbers*

	TBM n	TBM %[1]	CM n	CM %[1]	BLK n	BLK %[1]
Cods	350	8	203	26	241	27
Sculpins	835	25	137	17	0	0
Sand lance	213	6	271	34	325	36
Capelin	199	6	138	18	146	16
Righteye flounders	180	5	4	<1	0	0
Other fishes	271	8	16	2	6	<1
Shrimps	244	7	4	<1	34	4
Amphipods	910	27	12	2	0	0
Mysids	0	o	0	0	2	<1
Euphausiids	1	<1	0	0	0	0
Polychaetes	36	1	0	0	137	15
Other invertebrates	73	2	1	<1	14	2

c. *Estimated Grams Wet Weight*

	TBM n	TBM %[1]	CM n	CM %[1]	BLK n	BLK %[1]
Cods	2574	43	2210	59	2626	63
Sculpins	1555	26	414	11	0	0
Sand lance	497	8	694	19	975	23
Capelin	595	10	383	10	415	10
Righteye flounders	180	3	4	<1	0	0
Other fishes	130	2	32	<1	12	<1
Shrimps	122	2	2	<1	17	<1
Amphipods	312	5	2.4	<1	0	0
Mysids	0	0	0	0	<1	<1
Euphausiids	<1	<1	0	0	0	0
Polychaetes	36	<1	0	0	137	3
Other invertebrates	37	<1	<1	<1	7	<1

[1]**Numbers** indicate the percentage of stomachs containing food in which the food item was represented. Values in parentheses represent frequency in the total number of stomachs examined.

TABLE 3.   Importance   of major taxa in diets of thick-billed murres (TBM), common murres (CM) and black-legged kittiwakes (BLK) collected at Cape Lisburne, eastern Chukchi Sea, 1977-1980.

	TBM		CM		BLK	
	n	$\%^1$	n	$\%^1$	n	$\%^1$
Number examined	198	(100)	48	(100)	71	(100)
Number empty	16	(8)	3	(6)	4	(6)
Frequency of invertebrates	85	47	9	20	22	33
Frequency of fish	173	95	45	100	60	90

a. Frequency of Occurrence

Cods	99	54	35	78	28	42
Sculpins	89	49	10	22	4	6
Sand lance	75	41	25	56	29	43
Capelin	13	7	2	4	7	10
Righteye flounders	15	8	7	16	0	0
Other fishes	8	4	1	2	5	7
Shrimps	39	21	1	2	1	1
Amphipods	48	26	2	4	4	6
Mysids	19	10	3	7	0	0
Euphausiids	15	8	1	2	8	12
Polychaetes	12	7	0	0	13	19
Other invertebrates	11	6	I	2	2	3

b. *Numbers*

Cods	660	13	202	31	158	5
Sculpins	529	10	17	3	5	<1
Sand lance	838	16	255	39	263	8
Capelin	55	1	60	9	29	<1
Righteye flounders	123	2	83	13	0	0
Other fishes	22	<1	6	<1	7	<1
Shrimps	165	3	5	<1	1	<1
Amphipods	985	19	4	<1	1318	42
Mysids	295	6	9	1	0	0
Euphausiids	1544	29	6	<1	1626	51
Polychaetes	8	<1	0	0	51	2
Other invertebrates	25	<1	3	<1	2	<1

c. *Estimated Grams Wet Weight*

Cods	5028	51	1034	53	912	36
Sculpins	1135	12	18	1	30	1
Sand lance	2703	27	669	34	830	33
Capelin	132	1	122	6	87	3
Righteye flounders	123	I	83	4	0	0
Other fishes	44	<1	12	<1	14	<1
Shrimps	83	<1	2.5	<1	<1	<1
Amphipods	197	2	<1	<1	264	10
Mysids	59	<1	1.8	<1	0	0
Euphausiids	155	2	<1	<1	163	7
Polychaetes	8	<1	0	<1	52	2
Other invertebrates	13	<1	1.5	<1	1	<1

[1] Numbers indicate the percentage of stomachs containing food in which the food item was represented. Values in parentheses represent frequency in the total number of stomachs examined.

TABLE 4.   Fish biomass : invertebrate biomass in diets of thick-billed murres in the eastern Chukchi Sea.

Colony	June	1-20 July	21 July-10 Aug.	10-31 Aug.	Overall
Cape Thompson					
1976	2.9	15	8	11	8.4
1977	5.7	232	22	76	30
1978	---	---	---	59	---
1979	---	74	18	679	48
$\bar{x}$	4.3	107	16	206	29
s	2.0	112	7.2	316	20
Cape Lisburne					
1977	2.9	5.1	5.6	17	6.0
1978	---	9.0	9.3	637	11
1979		35	---	442	72
1980	---	---	372	---	---
$\bar{x}$	2.9	16	129	365	30
S	---	16	210	317	37

TABLE 5.   Average weight of major taxa in diets of thick-billed murres in the eastern Chukchi Sea, Units are g bird[1].

Colony	Taxon	1976	1977	1978	1979
Cape Thompson					
	Cods	14	10	DI[1]	14
	Sculpins	1.9	12	DI	4.4
	Sand lance	0.1	4.2	DI	2.1
	Capelin	o	o	DI	8.7
	Righteye flounders	0	0	DI	2.4
	Other fishes	1.7	0.8	DI	0.1
	Total fish	17	27	DI	32
	Total invertebrates	1.9	0.9	DI	0.7
Cape Lisburne					
	Cods	ND[2]	12	30	24
	Sculpins	ND	0.9	3.6	7.5
	Sand lance	ND	9.7	16	32
	Capelin	ND	0	0	1.8
	Righteye flounders	ND	0.02	1.5	0.6
	Other fishes	ND	0.4	0	0.6
	Total fishes	ND	23	51	66
	Total invertebrates	ND	3.9	4.5	n.9

[1]DI = data insufficient for meaningful comparison.
2ND = no data.

TABLE 6.   Percentage contribution of various taxa to total weight of fish
in diets of thick-billed murres in the eastern Chukchi Sea, 1976-1980.

Colony	June	1-20 July	21 Ju1Y-10 Aug	11-31 Aug
Cape Thompson				
Cods	74 ± 20	69 ± 48	45 ± 45	39 ± 32
Sculpins	24 * 21	6,7 ± 10	38 ± 47	36 ± 32
Sand lance	1 * 1.5	2,6 ± 3.3	5 ± 5.8	10 ± 19
Capelin	0	13 ± 23	10 ± 16	3 ± 6
Righteye flounders	0	6 ± 11	1.1 ± 1.8	2 ± 3
Other fishes	1 ± 1	1.5 ± 1.4	1.4 ± 1.1	9 ± 14
Cape Lisburne				
Cods	--	88 ± 10	49 ± 4	33 ± 28
Sculpins	--	3,4 ± 2.1	9.4 ± 2.2	12 ± 10
Sand lance	--	7 ± 5.8	38 ± .08	53 ± 34
Capelin	--	.7 * 1	o	1.5 ± 1.7
Righteye flounders	--	.3 ± .4	2.8 ± 4	.3 ± .4
Other fishes	--	.8 ± 1	.9 ± 1.3	.2 ± .4

TABLE 7.   Percentage contribution of various taxa to total weight of
fish in diets of black-legged kittiwakes in the eastern
Chukchi Sea, 1976-1980.

Colony	1-20 July	21 July-10 Aug.	11-31 Aug.
Cape Thompson			
Cods	84 ± 25	2 2 * 7	7.7 ± 6. 8
Sand lance	, 7 * 1	23 ± 19	87 ± 9
Capelin	14 ± 25	55 ± 26	4,8 ± 8
Cape Lisburne			
Cods	75 ± 19	14 ± 12	--
Sand lance	25 ± 20	72 ± 28	--
Capelin	o	9. 2 ± 16	--

TABLE 8.   Percentage contribution of various taxa to total weight of
invertebrates in diets of thick-billed murres in the
eastern Chukchi Sea, 1976-1980.

Colony	June	1-20 July	21 July-10 Aug.	11-31 Aug.
Cape Thompson				
Shrimps	69 ± 17	38 ± 17	50 ± 28	54 ± 23
Amphipods	6 ± 5	25 ± 42	18 ± 27	11 * 11
Polychaetes	18 ± 12	28 ± 26	9 ± 10	14 ± 13
Cape Lisburne				
Shrimps	27	20 ± 19	17 ±17	8.4 ± 7.9
Amphipods	11	5.5 * .5	42 ± 40	73 ± 16
Mysids	0	12 * 15	6.4 ± 3.7	0
Euphausiids	22	57 ± 23	32 ± 31	0
Polychaetes	27	1.2 ± 1.3	.7 ± 1.2	0

TABLE 9.   Percent weight of cod in combined weight of cods, sand lance
and capelin in diets of black-legged kittiwakes in the
eastern Chukchi Sea.

Colony	1-20 July	21 JulY-10 Aug.	11-31 Aug.
Cape Thompson			
1976	100	ND[1]	NF[2]
1977	>99	26	15
1978	NF	6	ND
1979	55	17	2
Cape Lisburne			
1977	97	1	ND
1978	70	23	ND
1979	59	ND	NO
1980	ND	22	ND

[1]ND = no data.
[2]NF . no fish recovered from birds collected during interval.

TABLE 10.   Age-length relationships (derived by otol iths) and sex ratios of combined samples of Arctic cod caught in Simpson Lagoon and adjacent coastal waters, 1977-79,   Data are from Craig and Haldorson (1981).

	Fork Length (mm)				Sex Ratio	
Age	n	$\bar{x}$	range	SD	n	% female
1	196	84	54-110	13	0	--
2	101	128	88-177	20	87	52
3	86	162	120-196	19	86	71
4	16	182	129-203	21	15	80
5	8	212	153-250	36	7	100
6	4	240	198-257	28	4	75
To ta 1	411				199	

TABLE 11.   Age-length relationships (derived from otoliths) of fourhorn scu1 pi ns *(Myoxocephalus quadricornis)* i n Simpson Lagoon.   Da ta are from Craig and Haldorson (1981).

	Total Length (mm)			
Age	n	$\bar{x}$	range	SD
1	55	63	46-81	8
2	46	94	74-160	15
3	34	134	102-167	17
4	31	169	133-208	17
5	31	193	168-224	14
6	24	211	176-248	18
7	5	222	197-258	25
8	3	236	220-265	25
9	1	226	- -	- -

TABLE 12.   Age-length relationships (derived from otoliths) of saffron cod in Simpson Lagoon. Data are from Craig and Haldorson (1981).

	Fork Length (mm)			
Age	n	$\bar{x}$	range	SD
1	108	125	79-192	21
2	69	198	145-242	21
3	1	247	- -	- -
4	3	256	200-303	52

Table 13.   Summary of census results of murres in northern Alaska.[1]

Year	Cape Lisburne		Cape Lewis	Cape Thompson		Bluff	St. Lawrence Is.
	Raw	Standardized	Raw	Raw	Standardized	Average	Raw
1960				251,000	357,000		
1972							32,000
1975						70,000	
1976	130,000	184,000		157,000	199,000	50,000	16,000
1977	131,000	184,000	19,000	143,000	171,000	38,000	
1978	126,000	172,000				40,000	
				114,000	149,000	35,000	
1980	173,000	174,000				31,000	
1981	149,000	153,000	21,000			29,000	34,000

[1]Data are from Sections Va. VIIa.
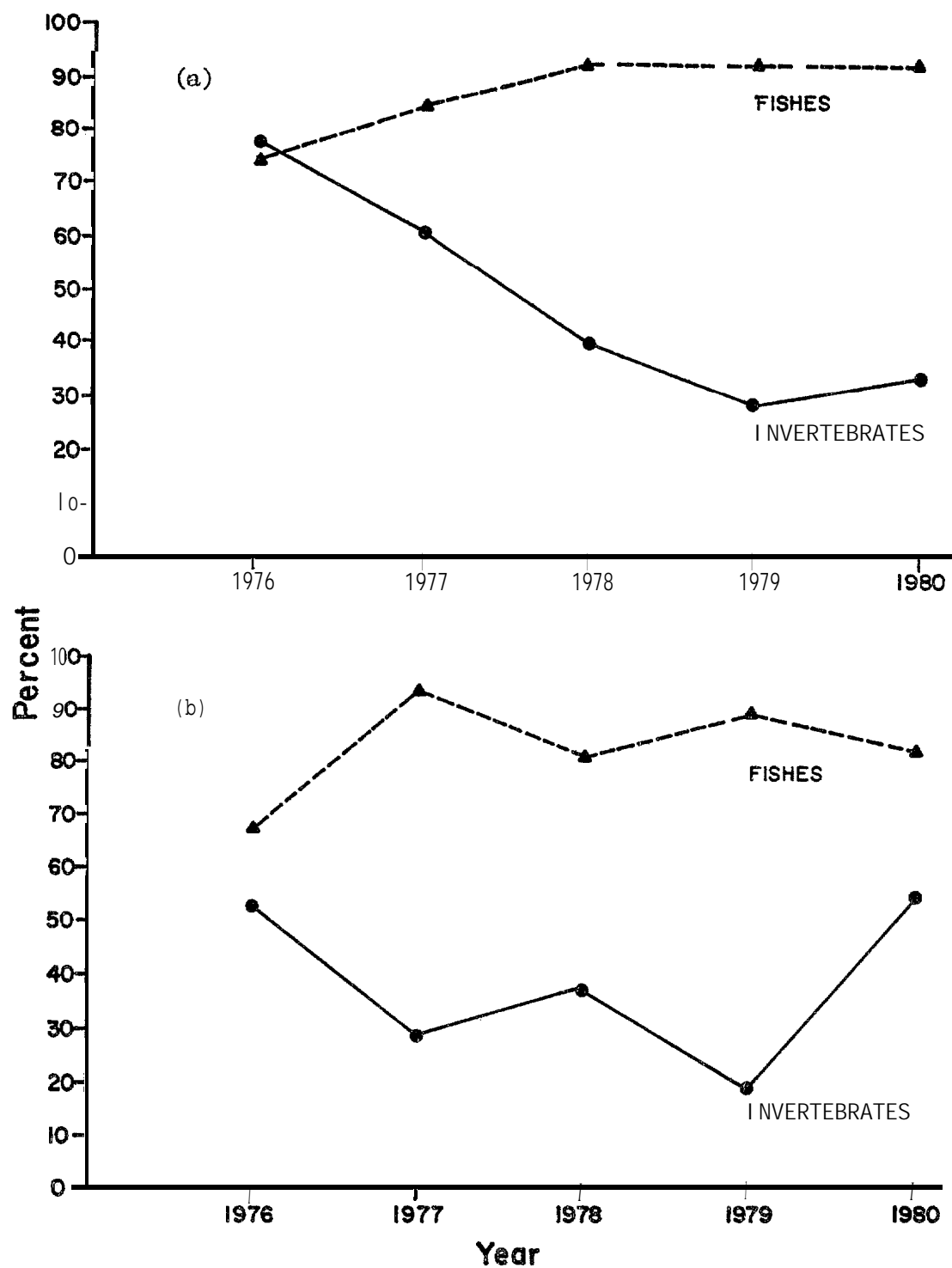
Figure 1. Frequency of occurrence of fish and invertebrates in diets of (a) thick-billed murres and (b) black-legged kittiwakes at Cape Lisburne and Cape Thompson.

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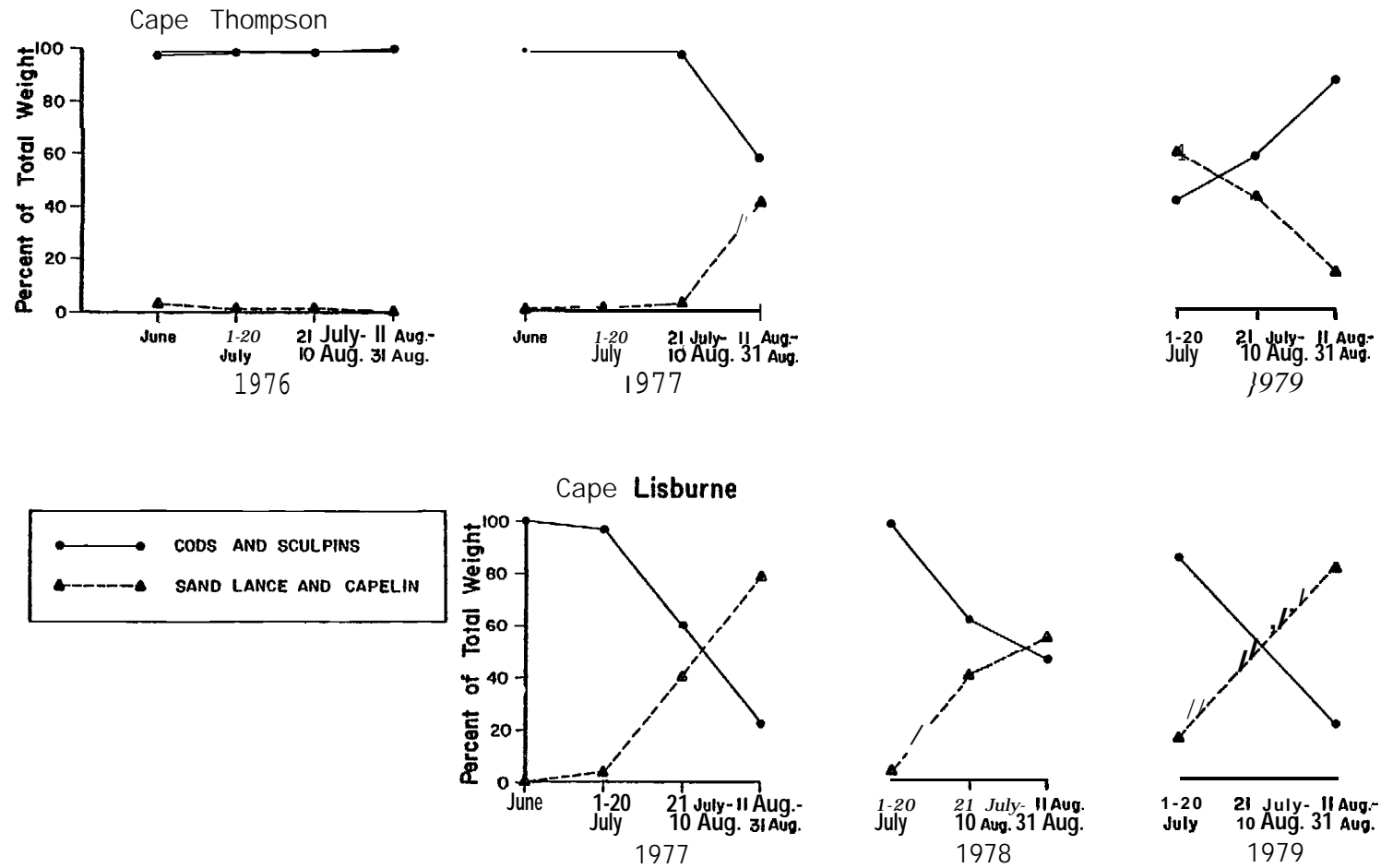
Figure 2. Combined importance of cods and sculpins compared to sand lance and capelin in diets of thick-billed murres at Cape Thompson and Cape Lisburne.
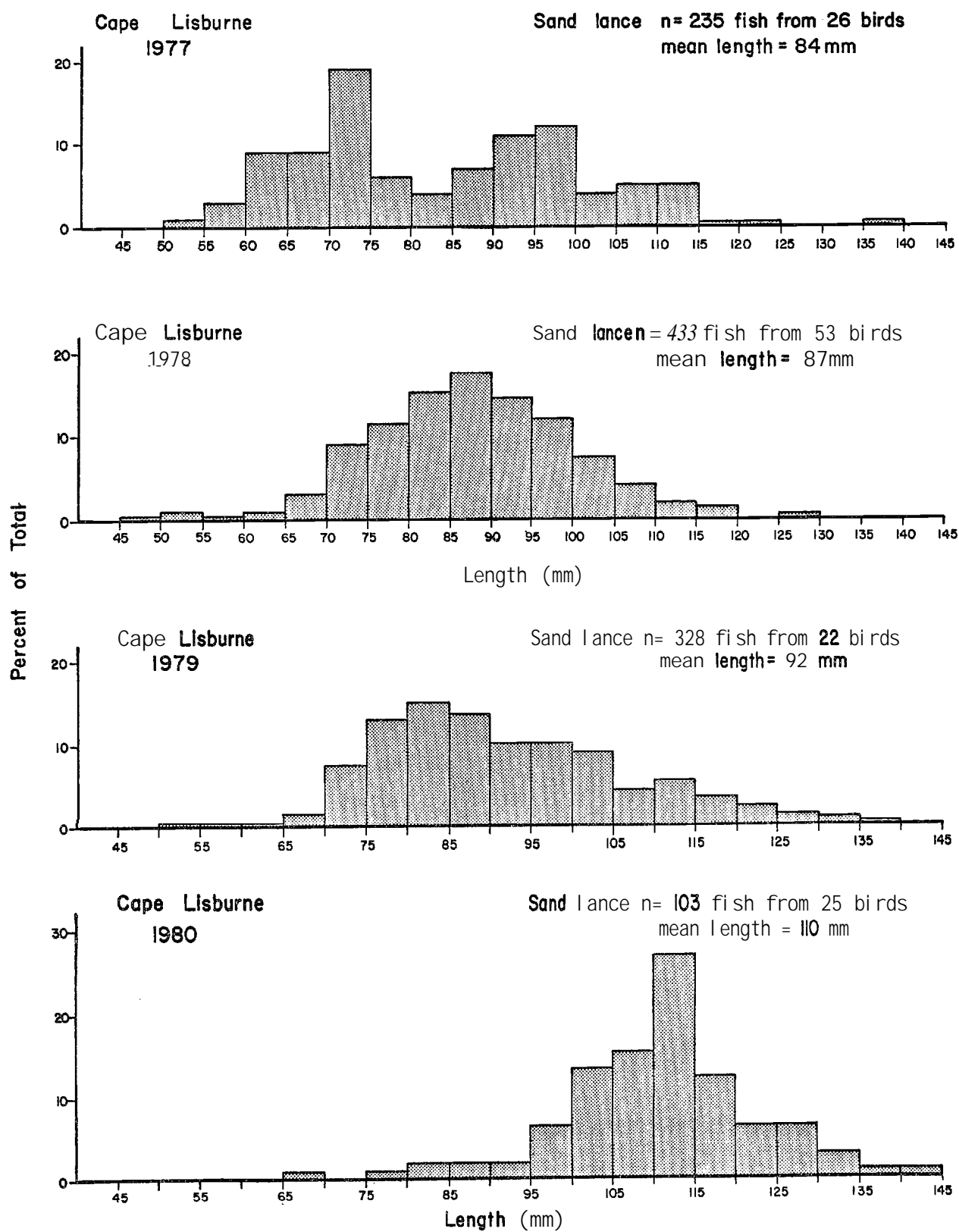
Figure 3.   Sizes of sand lance in diets of murres and kittiwakes at
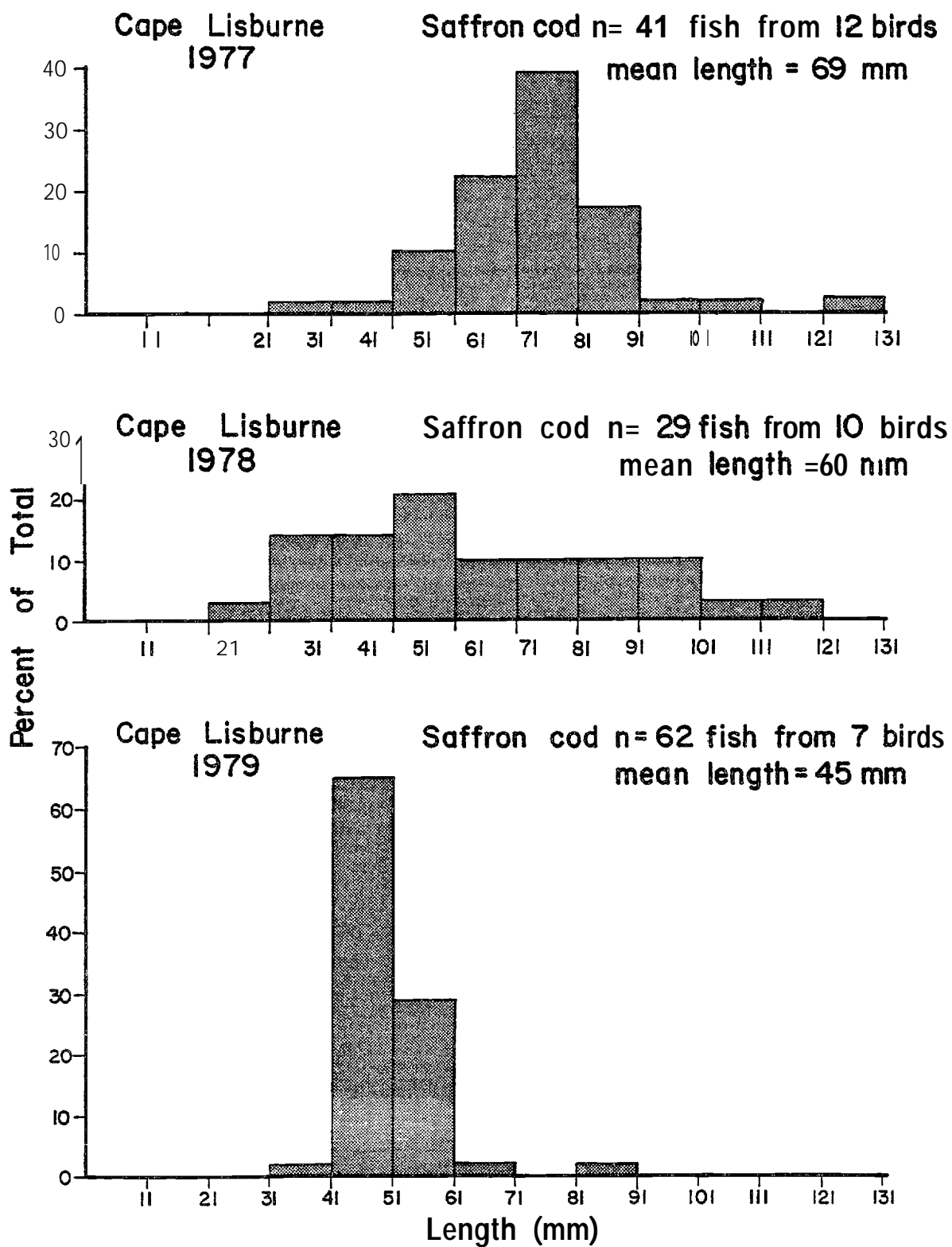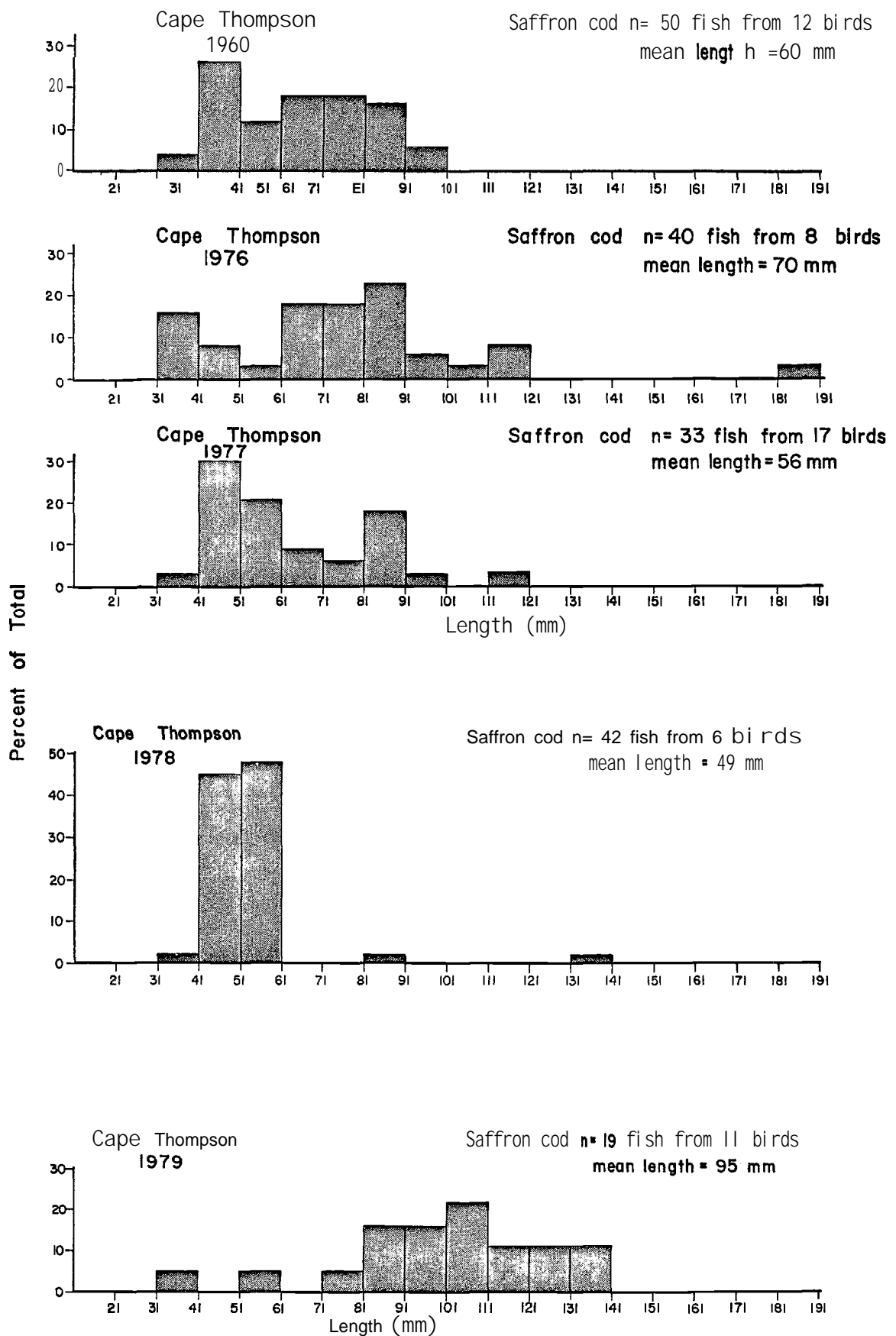   Cape Lisburne.

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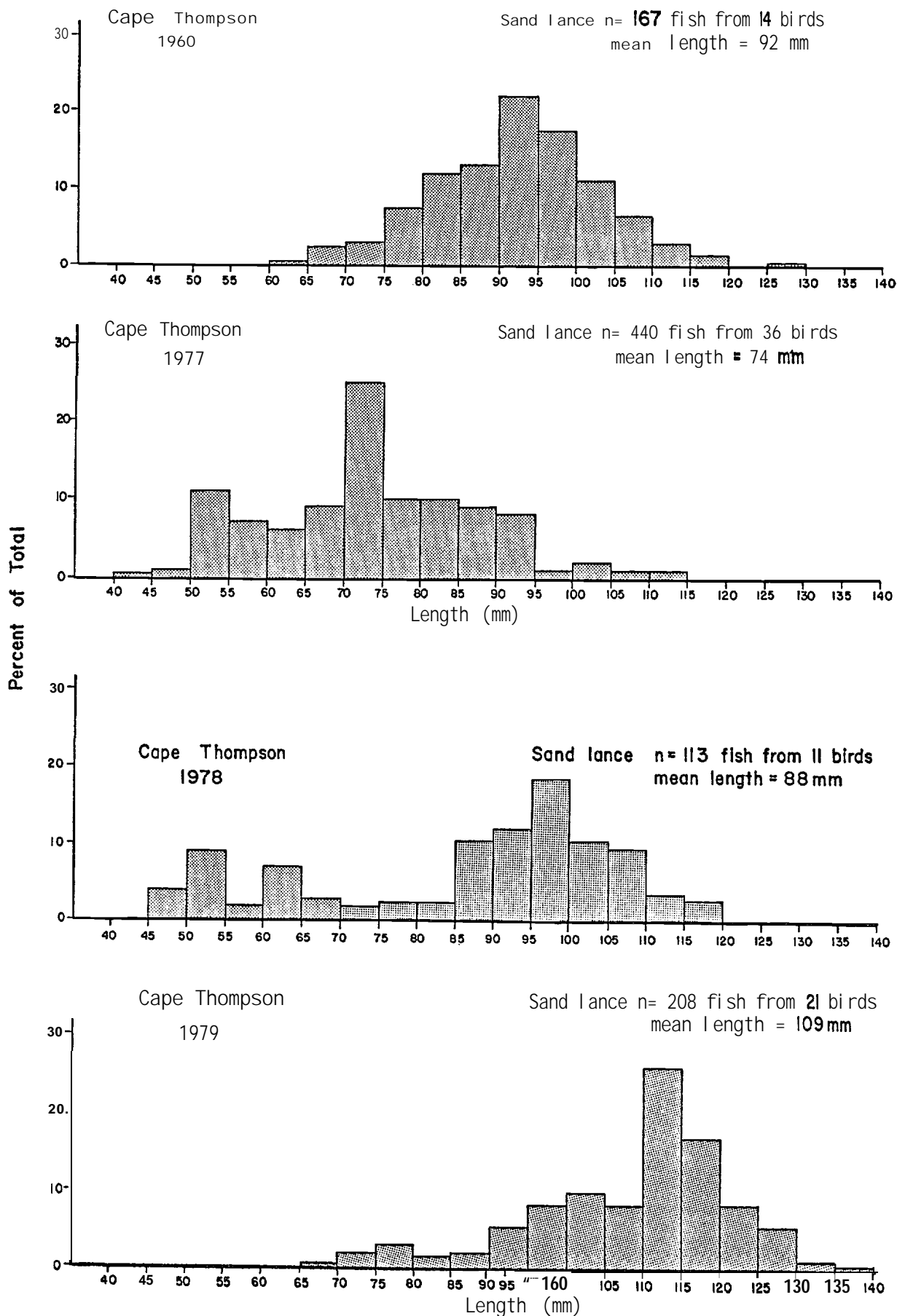
Figure 4. Sizes of sand lance in diets of murres and kittiwakes at Cape Thompson.

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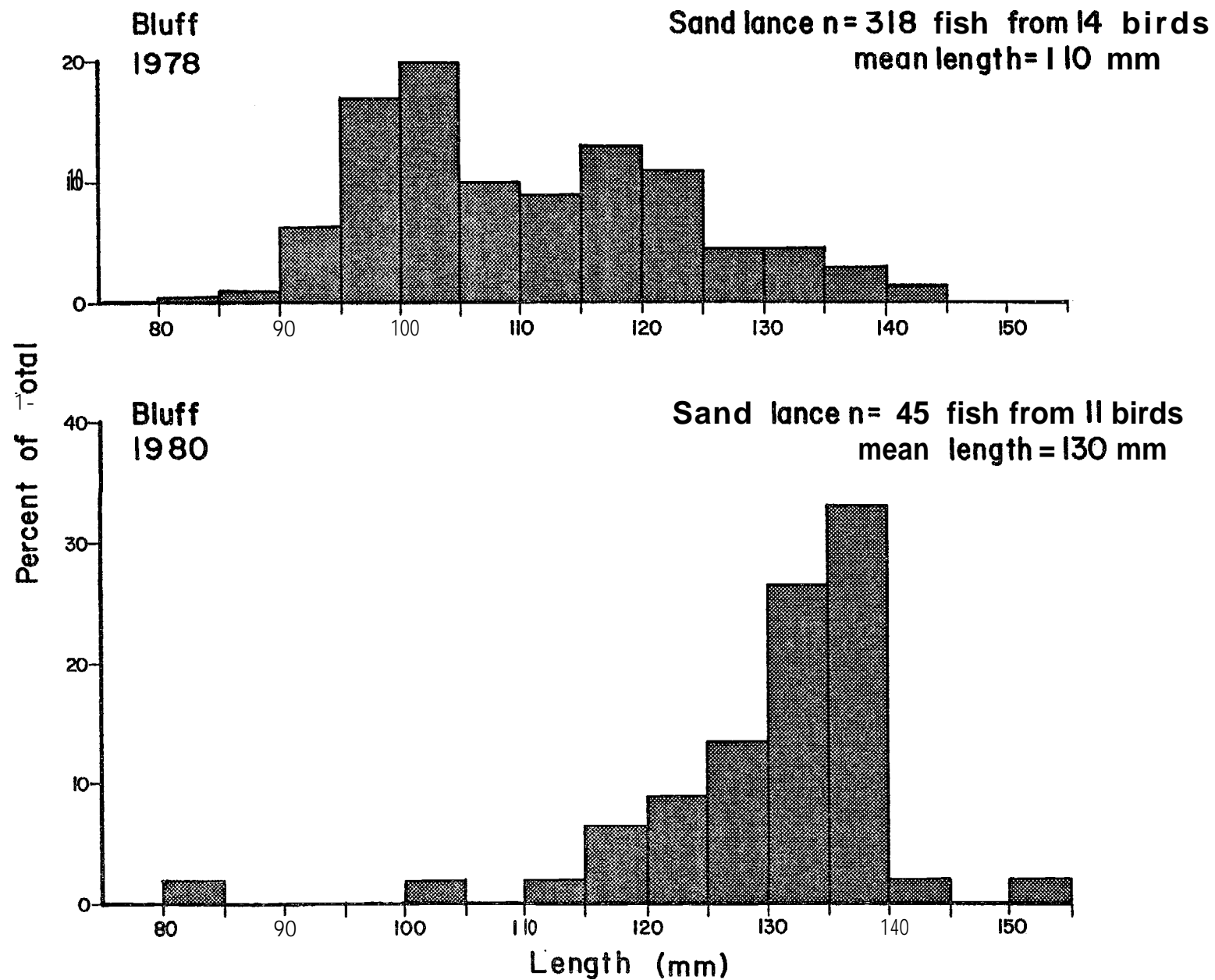
Figure 5. Sizes of sand lance in diets of murres and kittiwakes at Bluff.
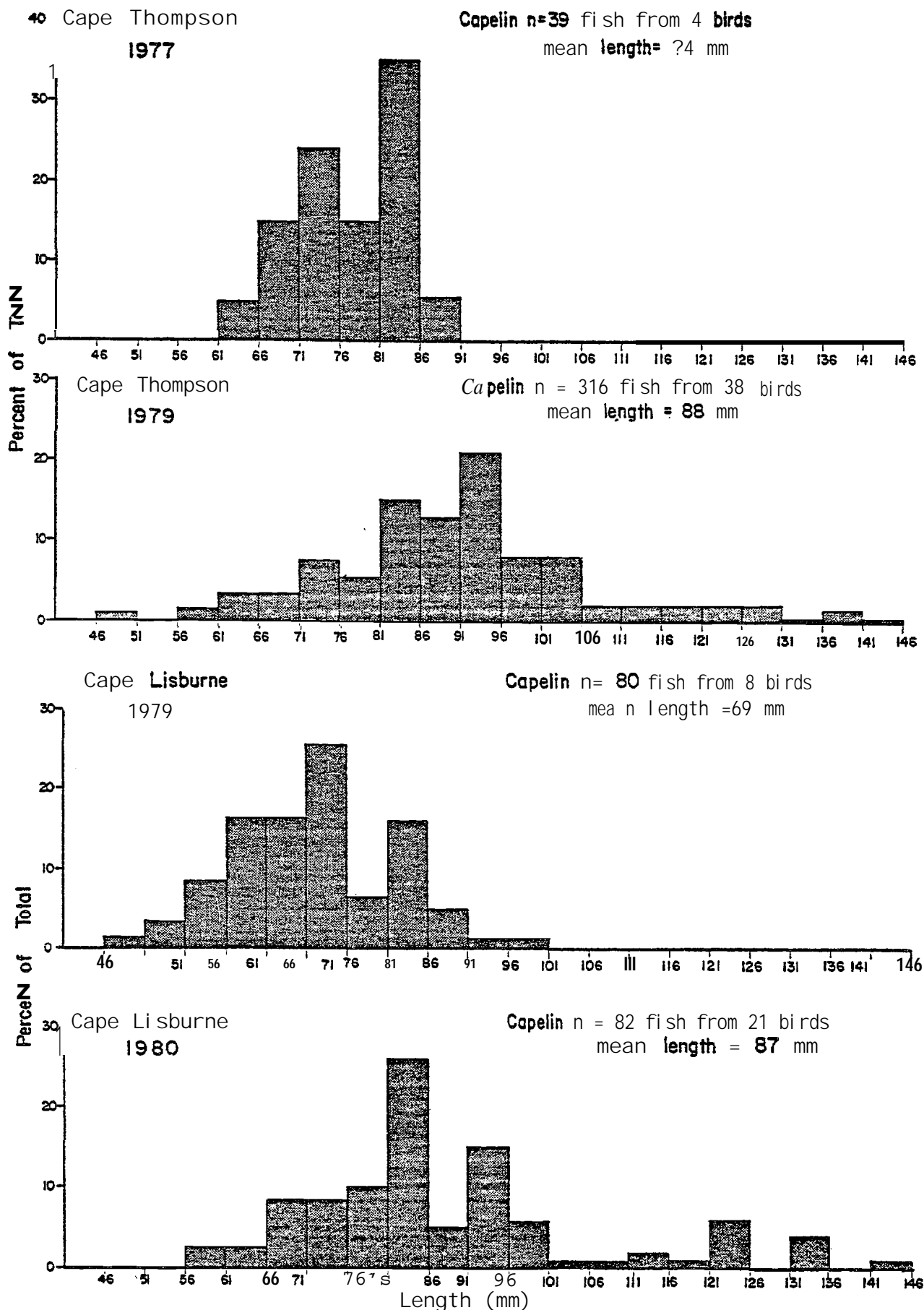
Figure 6. Sizes of **capelin** in diets of murres and kittiwakes at Cape Thompson and Cape Lisburne.
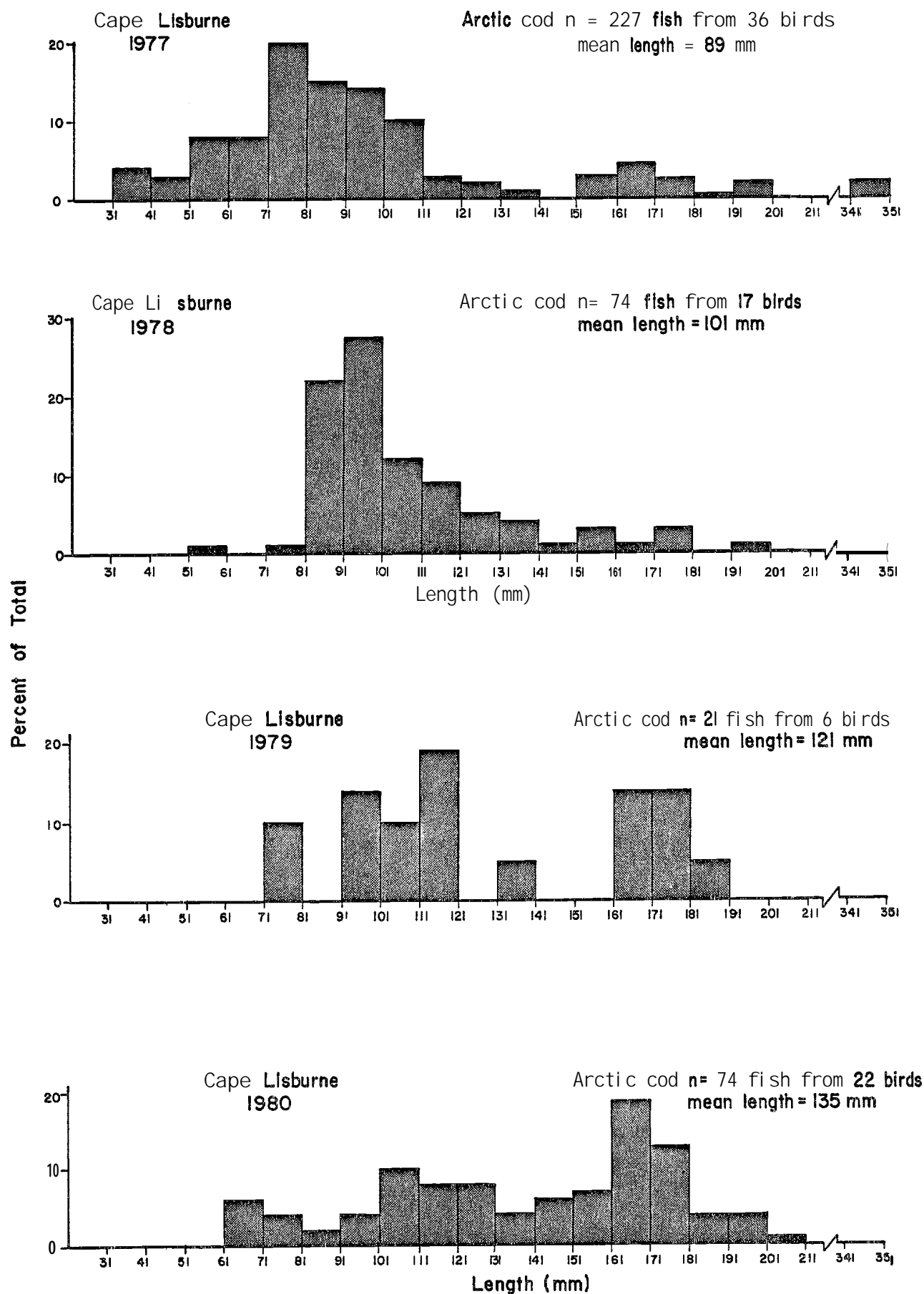
Figure 7. Sizes of Arctic cod in diets of murres and kittiwakes at Cape Lisburne.

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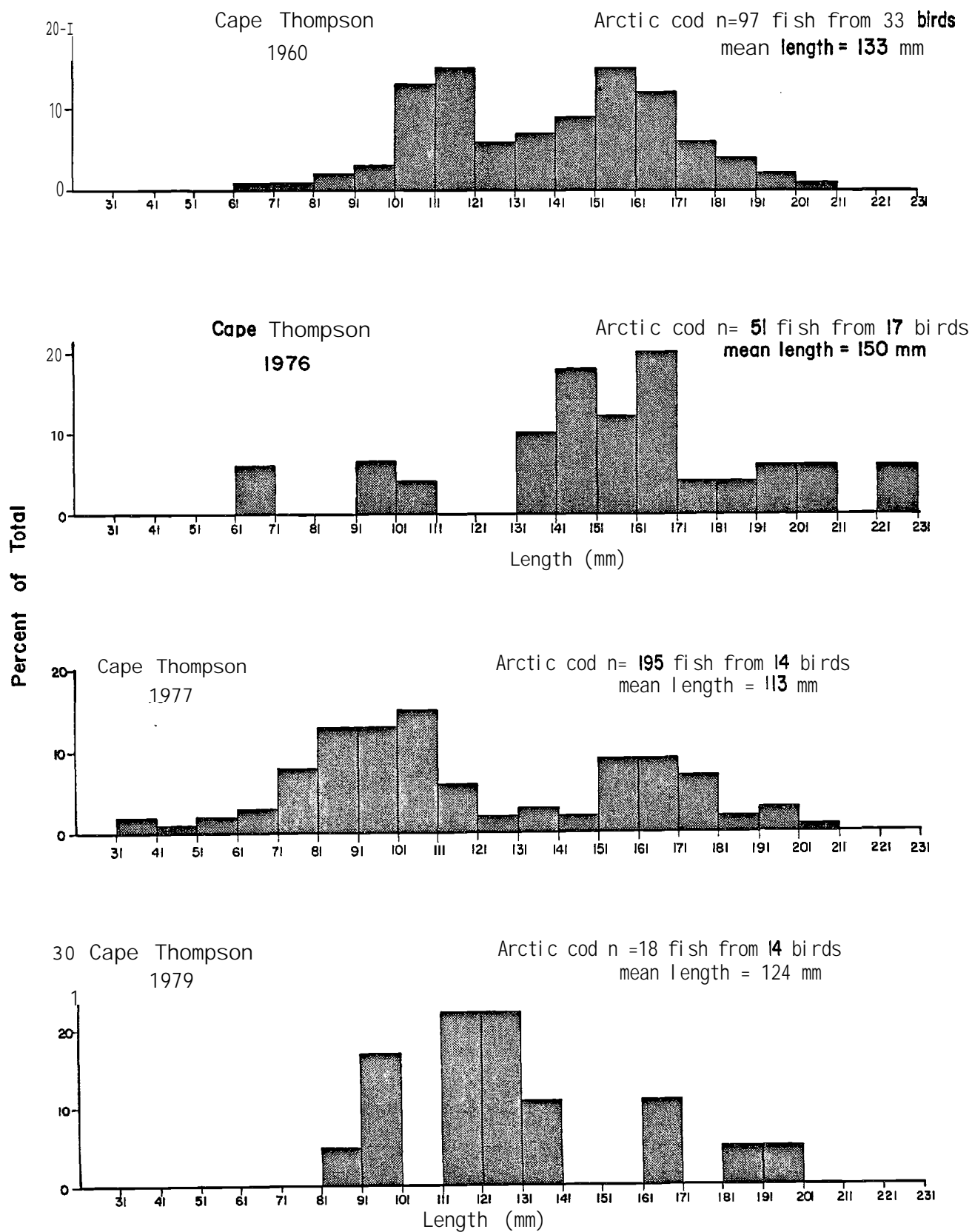
Figure 8. Sizes of Arctic cod in diets of murres and kittiwakes at Cape Thompson.
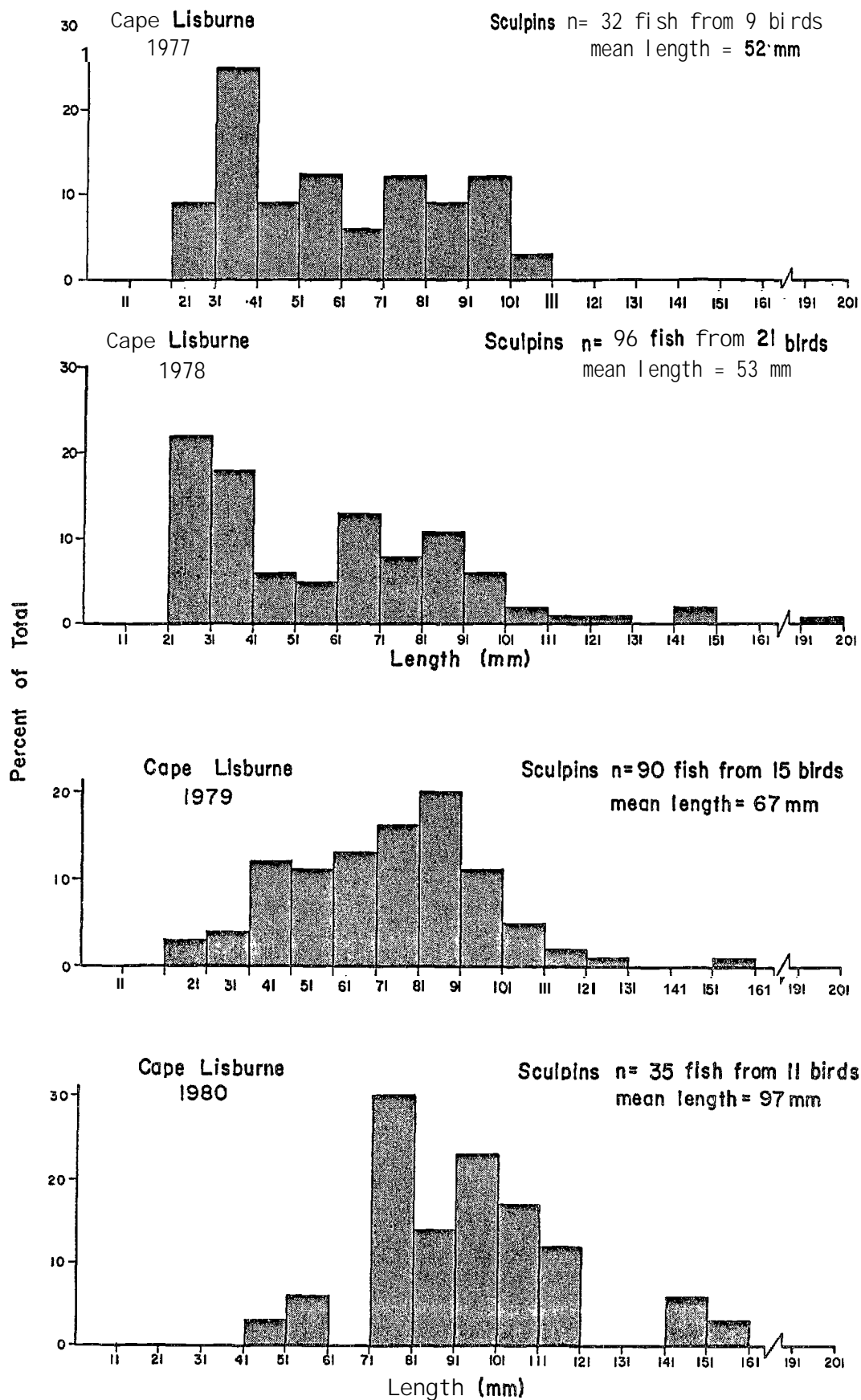
Figure 9. Sizes of sculpins in diets of murres and kittiwakes at Cape Lisburne.
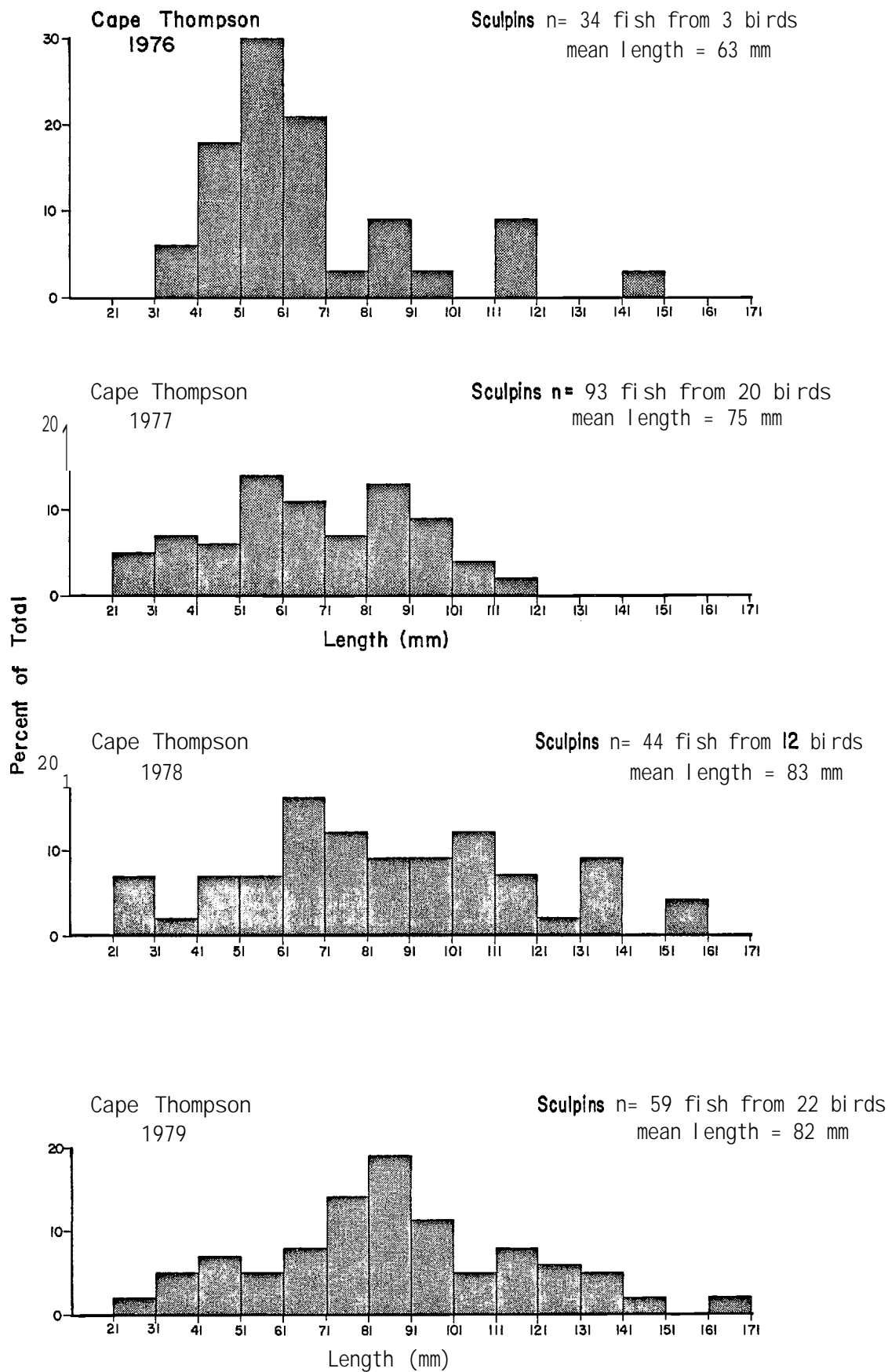
Figure 10.   Sizes of **sculpins** in diets of murres and kittiwakes at
Cape Thompson.

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Figure 11. Sizes of saffron cod in diets of murres and kittiwakes at Cape Lisburne.

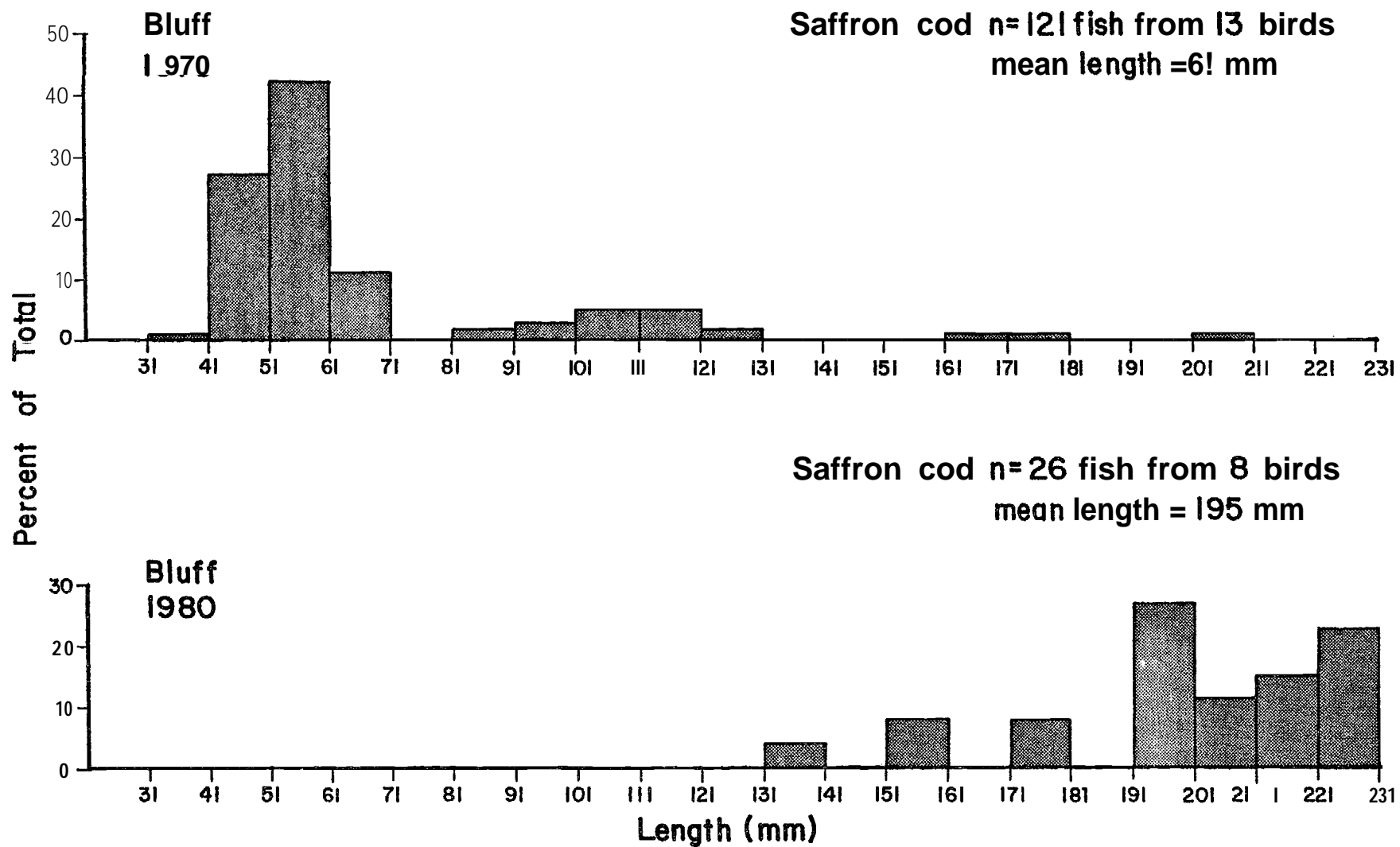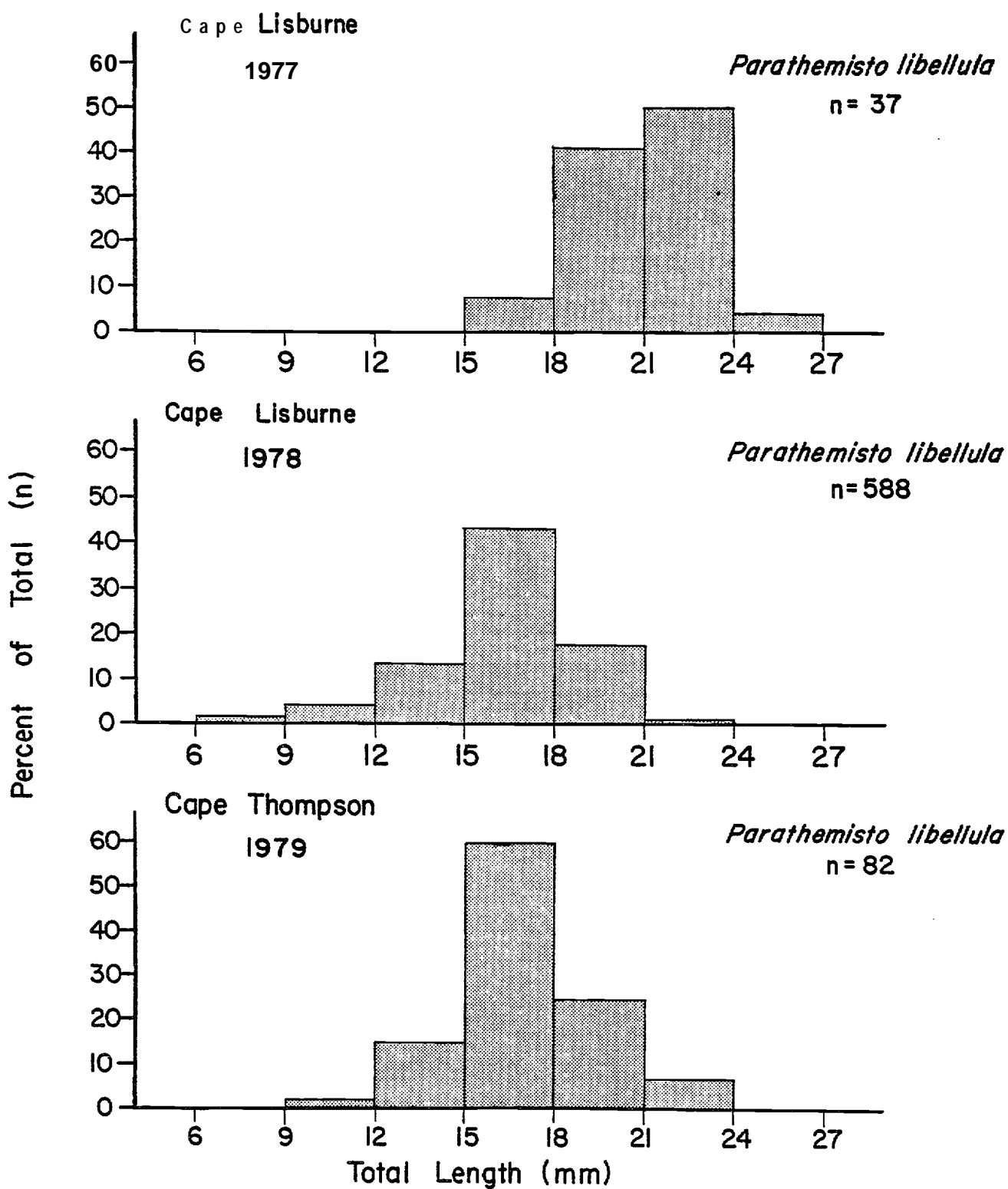Figure 12. Sizes of saffron cod in diets of murres and kittiwakes at Cape Thompson.

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Bluff
1970

Saffron cod n= 121 fish from 13 birds
mean length =61 mm

Percent of Total

50
40
30
20
10
0

31 41 51 61 71 81 91 101 111 121 131 141 151 161 171 181 191 201 211 221 231

Saffron cod n= 26 fish from 8 birds
mean length = 195 mm

Bluff
1980

30
20
10
0

31 41 51 61 71 81 91 101 111 121 131 141 151 161 171 181 191 201 21 1 221 231

Length (mm)

Figure 13. Sizes of saffron cod in diets of murres and kittiwakes at Bluff.

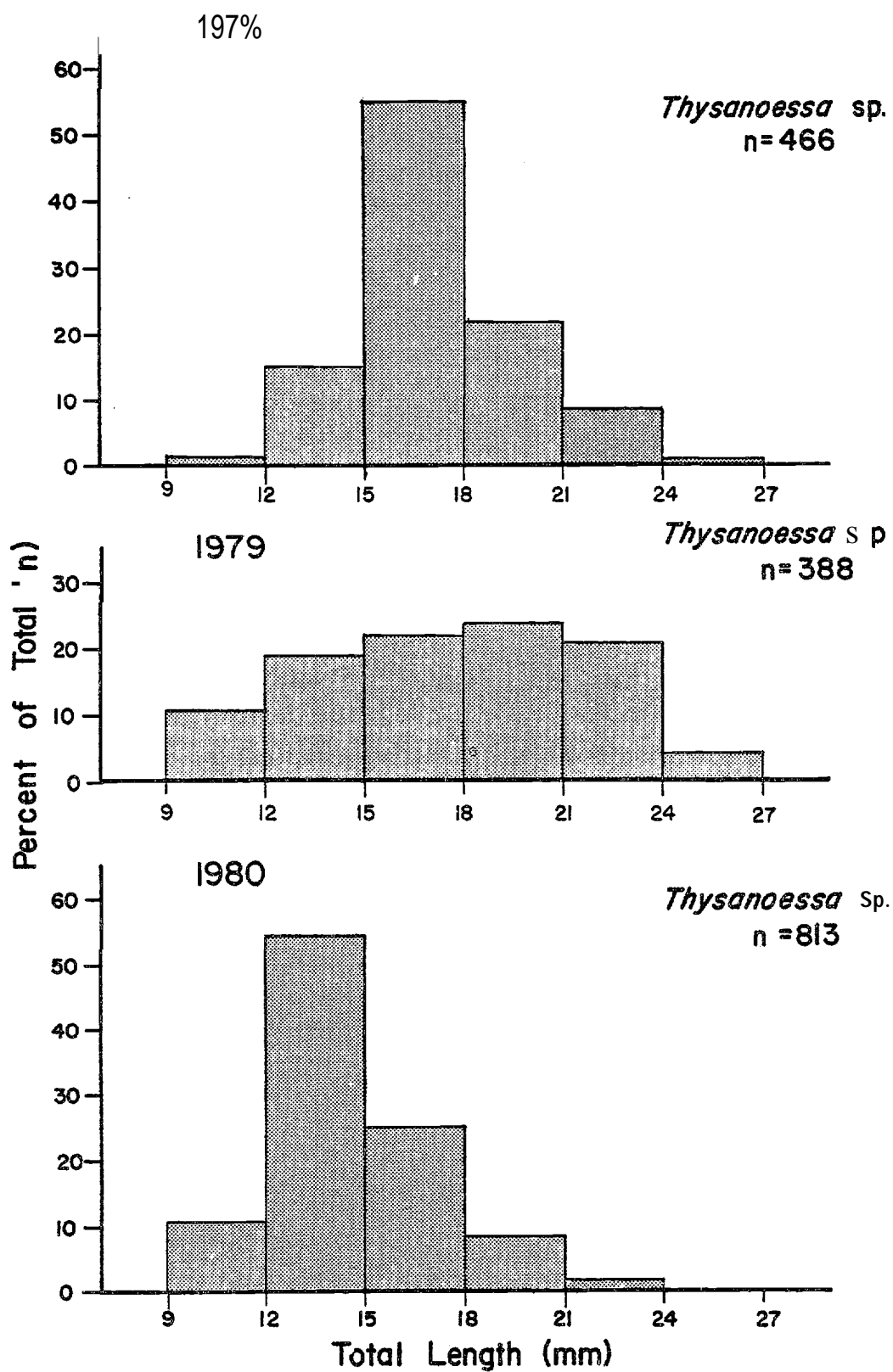Figure 14.   Sizes of *Parathemisto libellula* in diets of thick-billed murres at Cape Thompson and Cape Lisburne.

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Figure 15. Sizes of *Thysanoessa* sp. in diets of murres arid kittiwakes at Cape Lisburne.
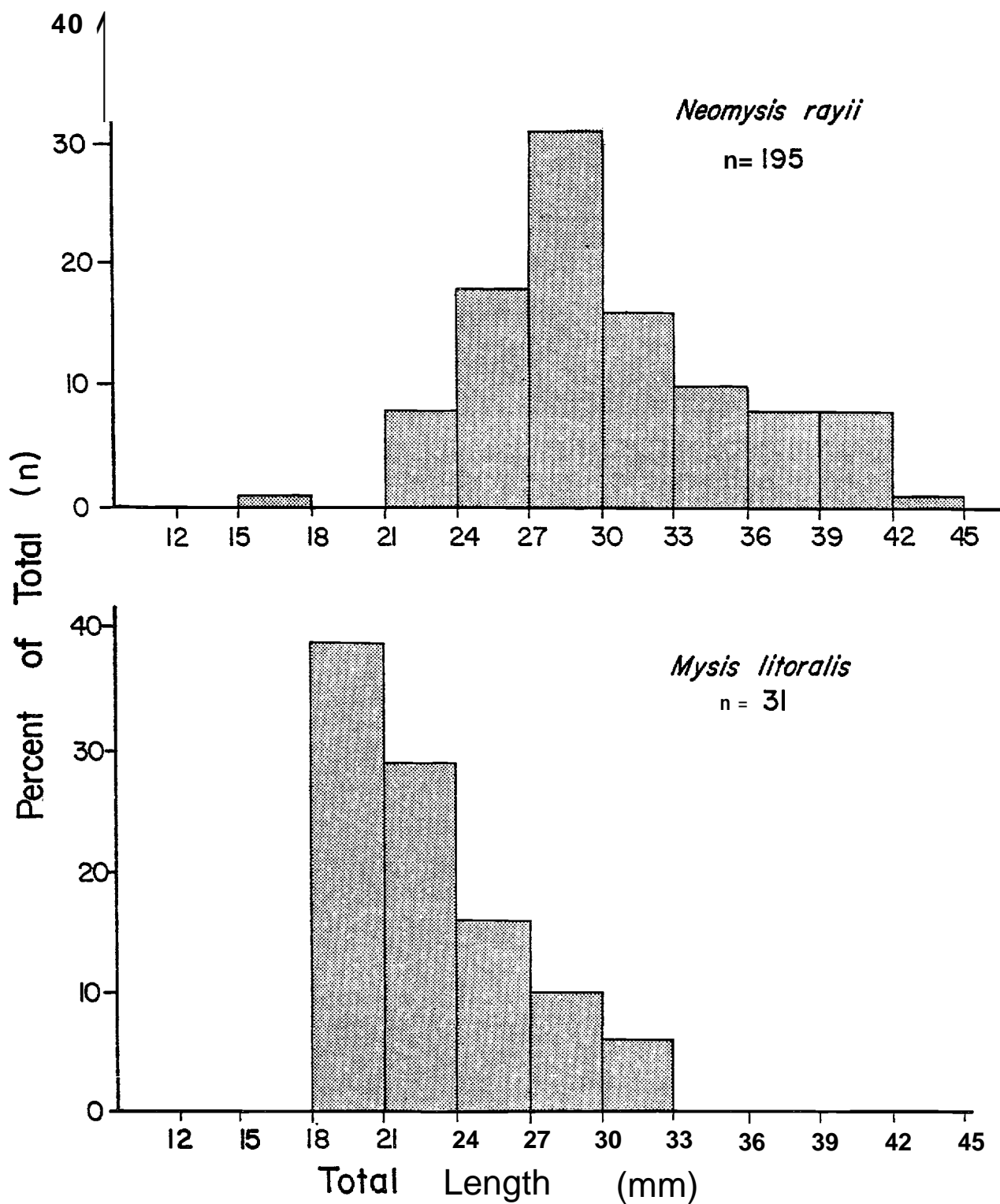
Figure 16. Sizes of mysids in diets of thick-billed murres at Cape Lisburne in 1978.
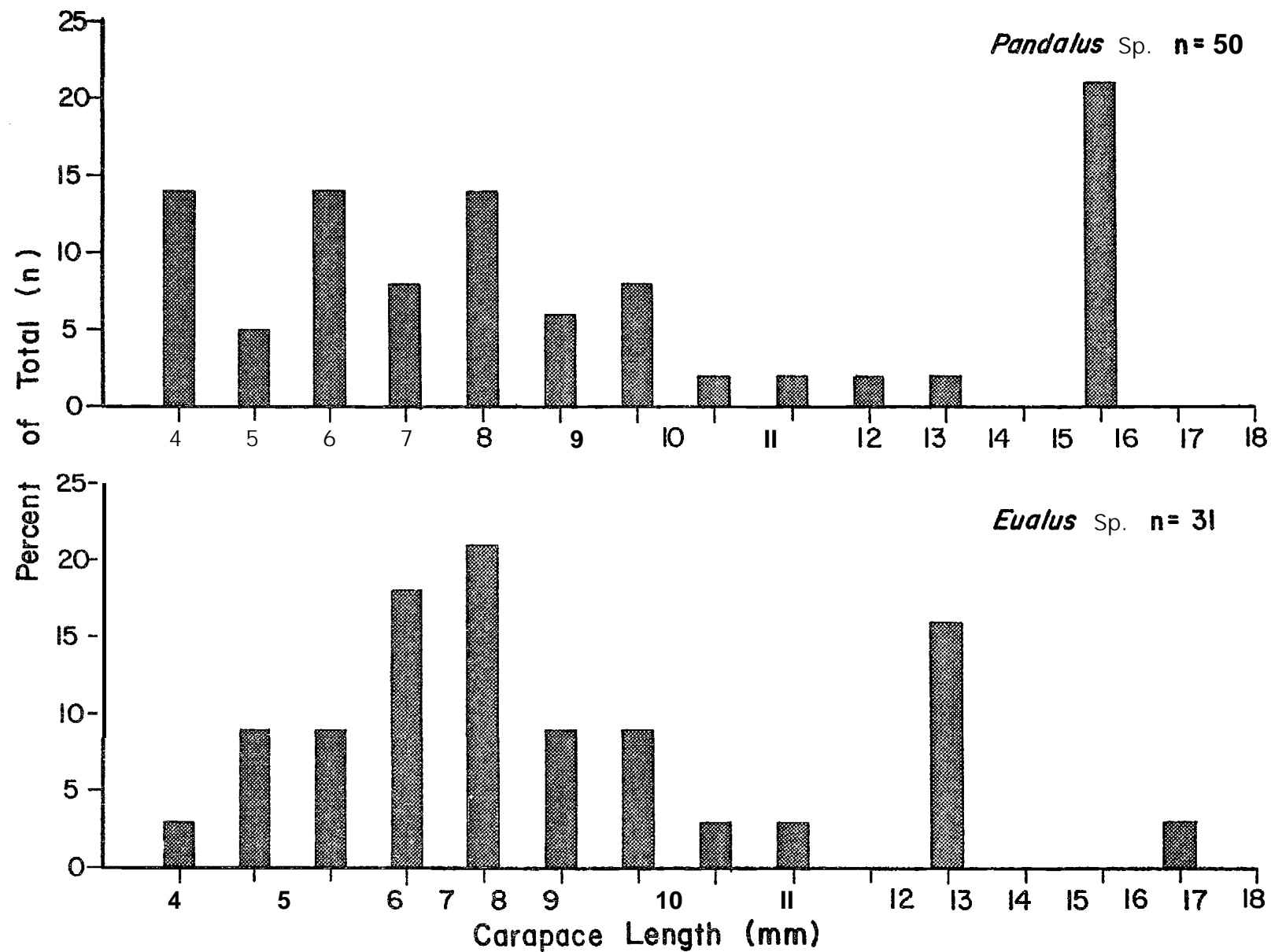
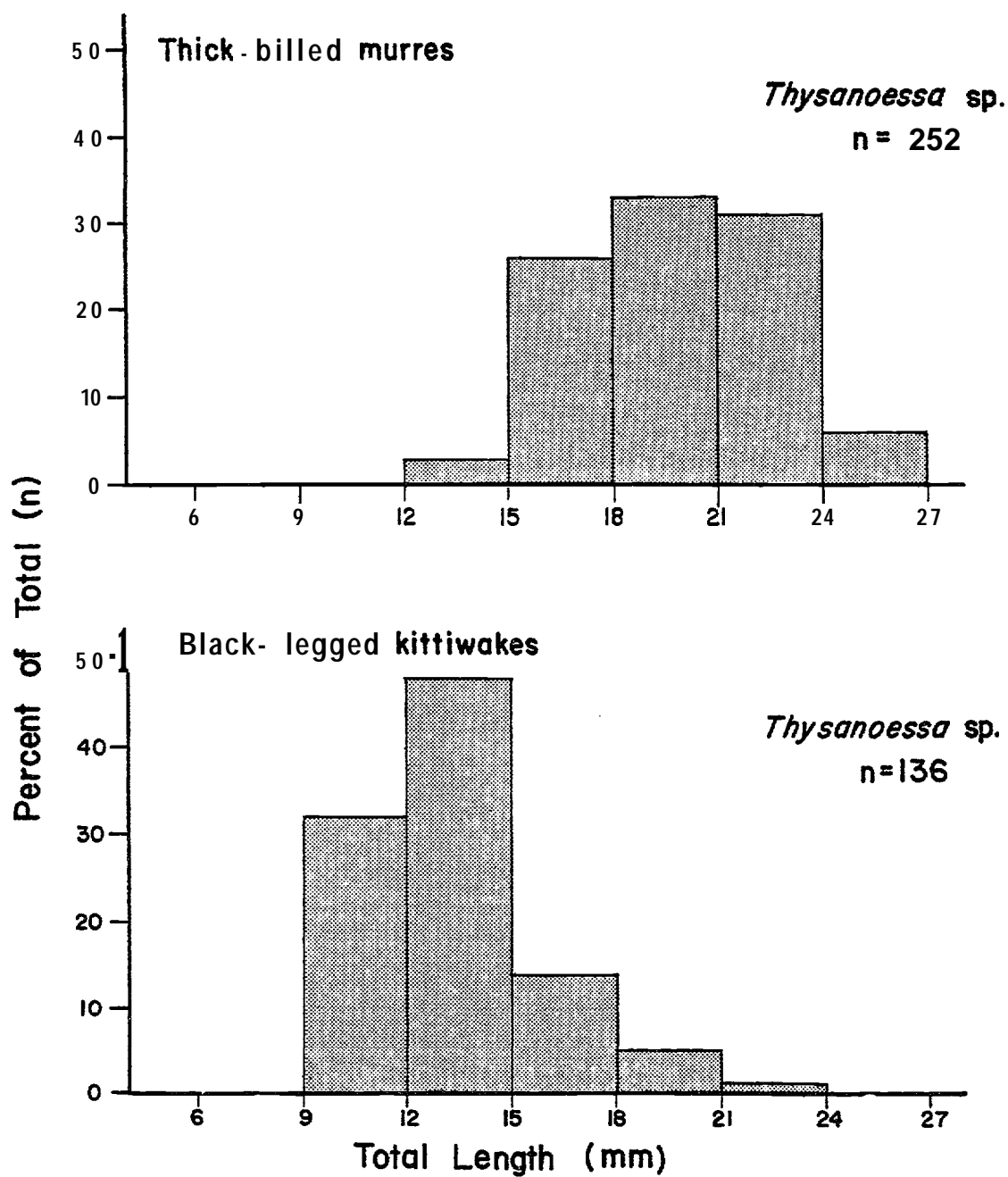Figure 17. Sizes of shrimps in diets of murres and kittiwakes at Cape Thompson and Cape Lisburne, 1976-1978.

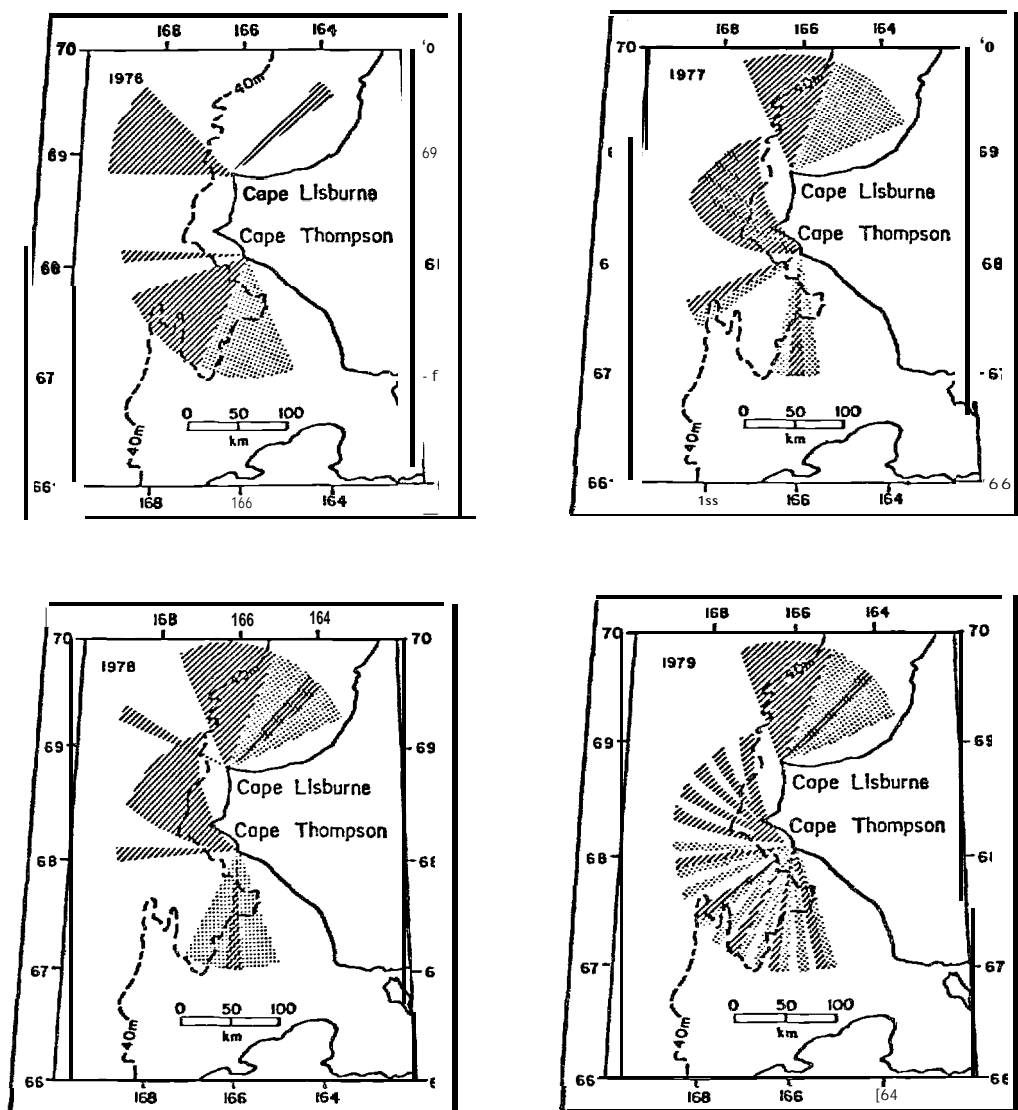Figure 18. Sizes of *Thysanoessa* sp. in diets of murres and kittiwakes at Cape **Lisburne** in 1978.

Figure 19. Directions taken by murres flying to and from foraging
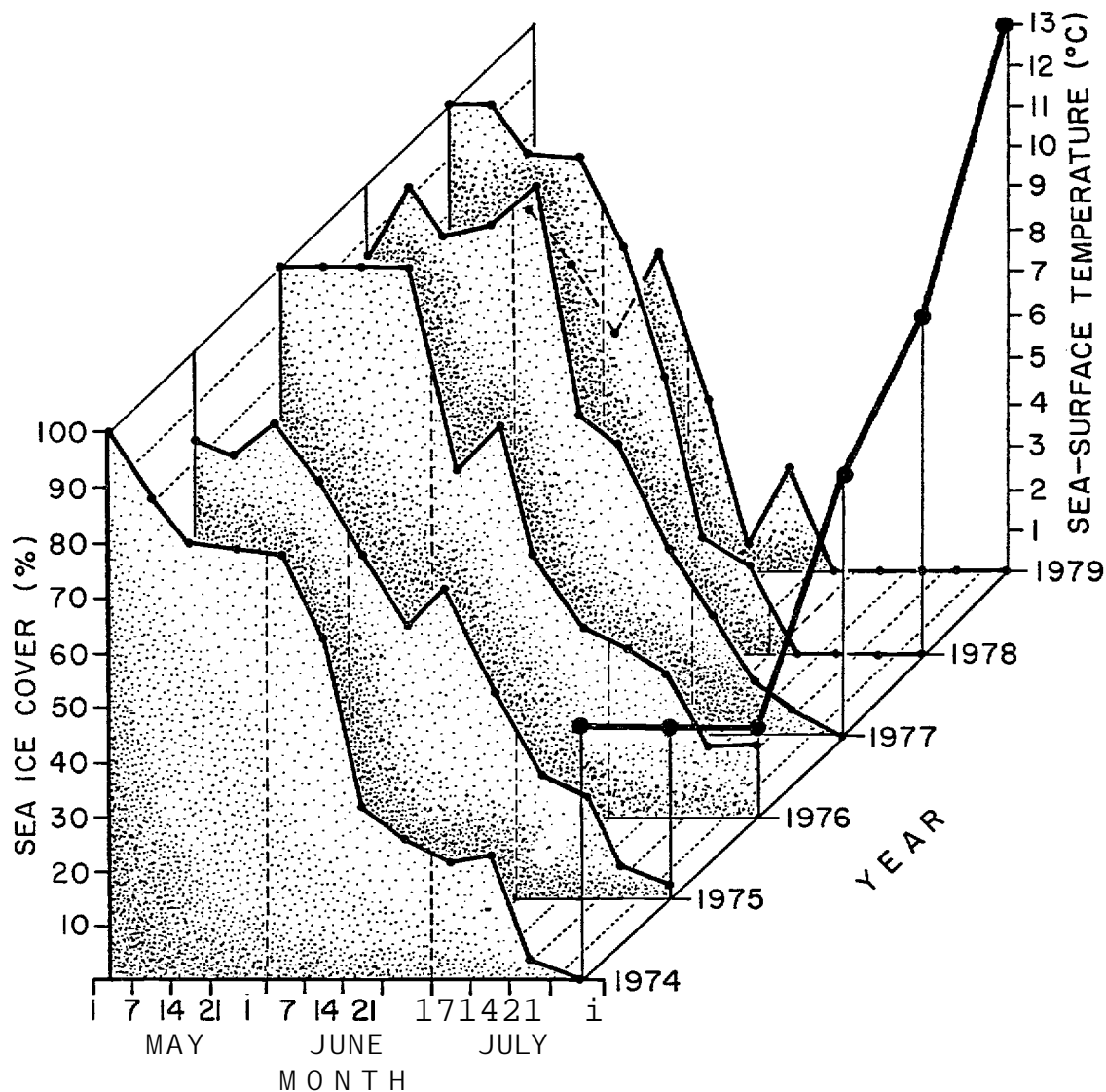areas in the eastern Chukchi Sea. Stipple = July,
bars = August.

Figure 20. Sea ice cover over the northern Bering Sea and eastern
Chukchi Sea, and sea-surface temperatures measured near
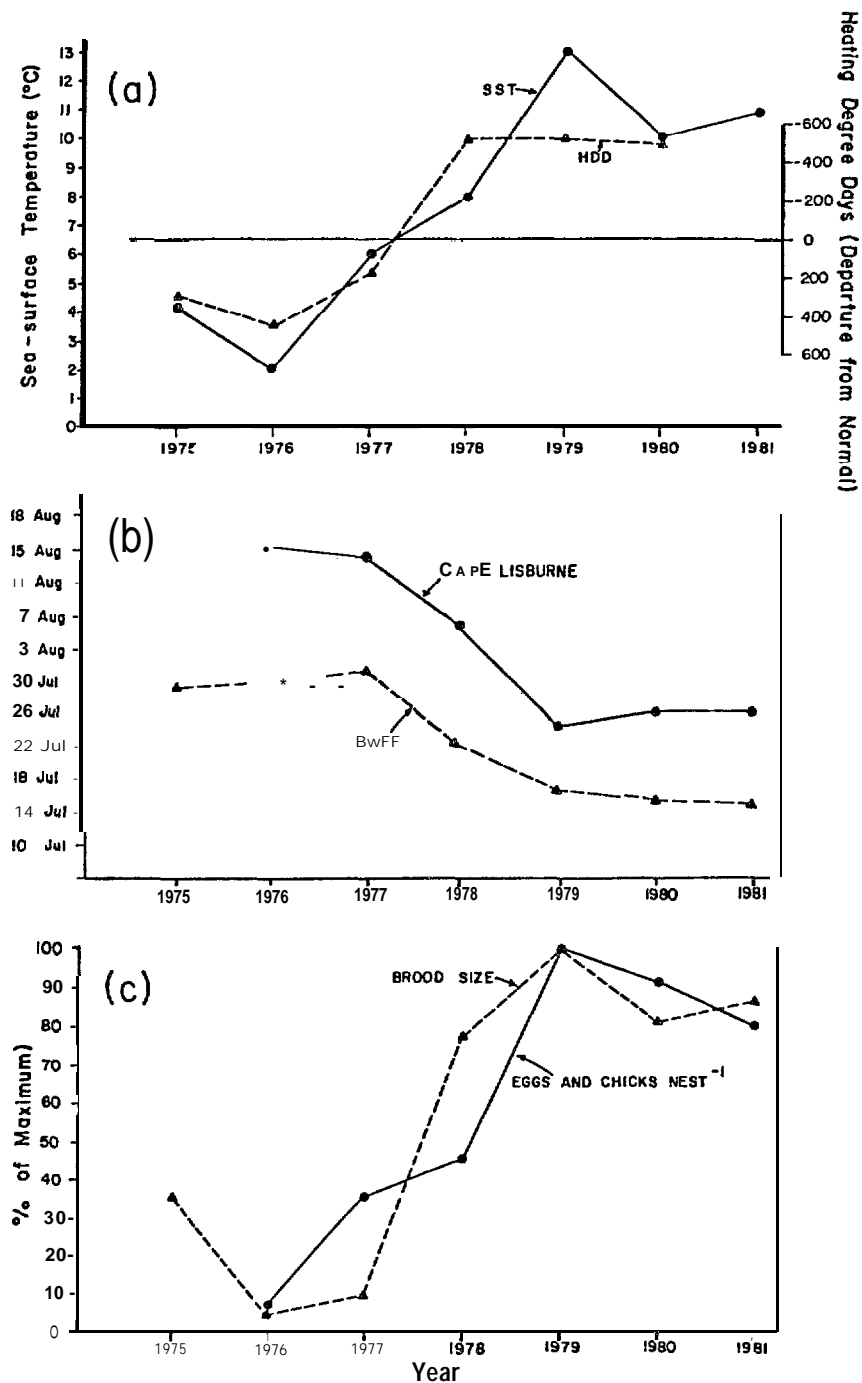Cape Lisburne (mean date = 16 July, s = 3 days).

Figure 21. Relationships between environmental change, kittiwake
nesting phenology and estimates of kittiwake reproductive
success at Cape Lisburne and Bluff. (a) Sea-surface
temperature near Cape Lisburne (mean date = 16 July,
s = 3 days), and departure from normal heating degree days
in April-July at Nome. (b) Mean date of hatch of kittiwake
chicks . (c) Numbers of kittiwake eggs and chicks nest^{-1}
in first week of hatching at Cape Lisburne (as a percentage
of maximum = 1.7 eggs and chicks nest^{-1}), and kittiwake
brood size in the late chick period at Bluff (as a per-
centage of maximum = 1.03 chicks nest^{-1}), Data for 1980
and 1981 at Bluff are from the early chick period; data
for 1975-1978 at Bluff are from Drury et al. 1981.

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Field work was conducted at Cape Thompson in 1976-1979, at Cape Lisburne in 1976-1981, at Cape Lewis in 1977, 1979 and 1981, at Bluff in 1979-1981 and on St. Lawrence Island in 1981. The locations of these colonies are shown in Figure 1, section IV.

The length of time we spent in the field varied from year to year and from colony to colony, and was often of short duration. In most years we arrived before or during the time that kittiwake eggs were hatching and stayed until the chicks were nearly grown. Exceptions to this schedule were 1979 and 1980 at Bluff when we arrived about 5-6 days after the peak of hatching, 1981 at Bluff when we departed shortly after the completion of hatching, 1978 at Cape Thompson when we visited the colony before egg laying and again after the chicks were approximately half grown, 1976 at Cape Lisburne when we arrived mid-way through the chick period, and 1979 at Cape Lisburne when we were away from the colony for about two weeks during the chick period.

Kittiwakes were censused by counting the number of adults present on the cliffs during the late incubation or chick period. Counts were by 1's, and were made from a raft by one or two observers using binoculars. We took three complete censuses of kittiwakes at Bluff in 1979 and two each season in 1980 and 1981. At Cape Thompson we took a complete census once each season in 1976, 1977 and 1979, and a partial census in 1978. Cape Lewis was censused completely in 1977 and 1981, and half of the colony was censused in 1978. The only complete census of Cape Lisburne was taken in 1977, although partial counts of that colony were made in 1978, 1979 and 1981.

Active nests, those nests that showed evidence of attention during the current breeding season, were counted at Cape Thompson at Colony 4 in 1978, and at Colonies 2-5 in 1979. Kittiwakes do not nest on Colony 1. Nests were counted on about 80% of the plots at Cape Lisburne in 1977, on a subset of six plots in 1978 and 1979, and 10 plots in 1981. Complete counts of nests were made at Bluff in 1980 and 1981, but nests were not counted colony-wide in earlier years.

Kittiwake nests on study plots were mapped and visited at varying intervals during the summer to obtain data on clutch size, brood size and chick growth rates. Chicks were weighed on Pesola spring balances. Growth rates were calculated for each chick by determining the slope of the regression equation relating all of the respective weights taken between the first weighing and the highest weight recorded that was less than or equal to 300 g. A preliminary analysis indicated that growth rates of most chicks remained linear through 300 g (also see Coulson and White 1958, Maunder and Threlfall 1972).

A prolonged period of adverse weather and our field schedule at Cape Lisburne in 1979 precluded nest checks between the day hatching began and 22 days later when all but two chicks weighed well over 300 g. We computed daily growth rates for Cape Lisburne in 1979 by (1) assuming

that the egg hatched the day after it *was* found pipped (see Maunder and Threlfall 1972), (2) assigning a weight of 35 g (the average weight of newly hatched chicks) for hatching weight, and (3) computing the daily weight gain between the presumed hatching day and the day the chick was first measured about three weeks later. Our preliminary analyses and other "accounts (e.g., Maunder and Threlfall 1972) suggest that daily weight gains typically decline soon after chicks reach 300-350 g; therefore the data on daily weight gains at Cape Lisburne in 1979 are minimum estimates and are not equivalent to those obtained in other locality-year samples.

Because we visited nests every several days, we frequently did not know the exact hatching date of particular chicks. In such instances we estimated the hatching date if the chick was weighed two or more times before attaining 300 g. Using the regression equation for daily growth rate, we calculated the date on which the chick would have weighed 35 g and used that value as the estimated hatching date for that chick. In some instances chicks were first weighed more than ten days later than the estimated hatching date, and we eliminated such individuals from the data base on hatching phenology. This method is unbiased if the growth rate is linear, or approximately so, between hatching and 300 g. Various studies (e.g., Coulson and White 1958, Maunder and Threlfall 1972) indicate that the growth rate of kittiwakes is linear from the time of hatching until about three weeks of age.

Before statistically analyzing the data on hatching phenology and growth rates of chicks we examined frequency distributions of each variable for each locality-year sample. In several cases, frequency distributions of hatching phenology and growth rates were skewed and/or kurtotic. Consequently we analyzed these variables nonparametrically, using the Kruskal-Wallis Test. We subsequently followed the Multiple Comparisons Procedure outlined by Conover (1980) to make pairwise comparisons among the samples.

We measured the length and maximum breadth of eggs at Cape Thompson in 1977 and 1979 and at Cape Lisburne and Bluff in 1981. We calculated egg volumes using the formula $0.4866 \times \text{length} \times \text{breadth}^2$ (see Coulson 1963). Coulson (1963) showed that the volume of eggs varies with respect to clutch size and position in the laying sequence. In Coulson's study volumes of eggs in one-egg clutches and the second egg in two-egg clutches were equivalent and about four percent smaller than the first egg in two-egg clutches. Since we typically first visited colonies after the completion of egg laying, we usually were unable to determine the laying sequence in multiple-egg clutches. Consequently we compared locality-year samples grouping the data by clutch size only and not by position in the laying sequence.

VIc. KITTIWAKES - RESULTS

Summaries of the kittiwake censuses, including counts of kittiwakes at Bluff in 1975-1978 (see Drury *et* al. 1981), are shown in Table 1. Beginning in 1978 at Cape Lisburne and Cape Thompson, and in 1979 at Bluff, kittiwake numbers began to increase over previous years and

remained higher at least through 1979 at Cape Thompson and through 1981 at Bluff and Cape Lisburne. A similar change occurred at Cape Lewis.

The number of nests at Cape Thompson in 1979 was similar to the number reported by Swartz (1966) for 1960 and 1961, although there were large discrepancies among the four colonies where kittiwakes nest (Table 2). The number of nests at Colony 4 in 1978 was nearly 50% lower than in the other three years of study; however, this difference may not have been representative of Cape Thompson as a whole. Nests on two plots at Colony 2 were also counted in 1978 and the total, 829, was only 5% lower than the total of 870 counted on the same plots in 1979. From counts of selected census plots at Cape Lisburne, we estimated that nests numbered about 14,000 in 1977, 14,500 in 1978, 14,400 in 1979 and 13,300 in 1981. Numbers of active nests on three study plots where nest contents were monitored were 79, 76, 75 and 71 in 1978-1981, respectively. These counts and our estimates of total nests indicate little variation in the numbers of kittiwake nests among years at Cape Lisburne. At Bluff, the numbers of nests, as well as the numbers of individuals, were nearly the same in 1980 and 1981, about 8,500 and 8,300, respectively.

Replicate counts of kittiwakes on three census plots at Colony 4 at Cape Thompson in 1976 demonstrated great daily variation in attendance of adult birds. Totals of 467, 75 and 734 adults were counted at 1845 h (Bering Daylight Time) on 9 August, 1750 h on 14 August and 1835 h on 15 August, respectively. Searing (1977) reported that kittiwake numbers also varied considerably between days on St. Lawrence Island in 1976, and Drury et al. (1981) reported similarly erratic attendance patterns the same year at Bluff. In 1979 at Bluff, we counted kittiwakes on five areas at the same times on several days (Figure 1). Day-to-day variation in numbers was slight; overall, numbers in mid-afternoon fluctuated between 110% and 124% of the number of nests during the 17-day period.

Mean hatching dates of the chicks we weighed for growth rates are shown in Figure 2. Significance relationships among colonies and years are presented in Table 3. Three trends are apparent from these data: (1) hatching dates were progressively earlier from 1976-1977 through 1979, after which time they stabilized, (2) hatching dates within years were progressively earlier with decreasing latitude and (3) hatching synchrony among nests tended to be higher in later years than in earlier years.

As hatching dates, and thus laying dates, became earlier each year, egg production by laying females increased (Table 4). These data are not strictly comparable between years and colonies since we generally arrived relatively late in the breeding season and an unknown number of eggs probably had already been lost (see Swartz 1966). Still, they indicate the magnitude of change in clutch size that occurred between 1976 and 1979.

Table 4 also lists clutch sizes of black-legged kittiwakes on the Pribilof Islands (St. Paul Island and St. George Island) obtained by Hunt et al. (1981) in 1975-1979. Egg production on the Pribilof Islands was much more constant among years, never falling as low or rising as high as

production in the northern colonies. Such a pattern is consistent with the uniform laying and hatching dates on the Pribilof Islands, which varied less than a week in the years 1975-1979 (Hunt *et al.* 1981).

The number of nests that contained eggs at the northern colonies also increased after 1976 (Figure 3). That increase and larger clutch sizes led to much improved levels of productivity by 1979 (Figure 4). Many kittiwakes also laid large clutches in 1980 and 1981, but a higher incidence of chick death in those years resulted in low levels of reproductive success compared to 1979. Hunt *et al.* (1981) reported that productivity of black-legged kittiwakes (expressed as the ratio of chicks fledged to nesting attempts) fluctuated between 0.36 and 0.54 on St. Paul island in 1975-1979 and between 0.22 and 0.62 on St. George Island in 1976-1978. Like phonological dates and clutch sizes, productivity on the Pribilof Islands was much more stable than in the northern colonies and was about midway between the lowest and highest levels we observed (see Figure 4).

Growth rates of kittiwake chicks were generally high, except in 1977 at Cape Thompson and in 1981 at Bluff and Cape Lisburne (Table 5). Growth rates at Cape Lisburne in 1980 were lower than in 1977, but higher than in 1981. Significance relationships of chick growth rates among all colonies and years are shown in Table 3.

As a group, growth rates of kittiwake chicks in northern Alaska were much higher than rates reported elsewhere. Hunt *et* al. (1981) reported growth rates ranging between 11.5 ± 2.6 g day^{-1} (n = 24) and 16.6 ± 2.9 g day^{-1} (n = 14) for black-legged kittiwake chicks on the Pribilof Islands in 1975-1979. Growth rates of kittiwake chicks in Newfoundland were about 13-15 g day^{-1} (Maunder and Threlfall 1972). Coulson and White (1958) reported that growth rates of kittiwake chicks at a colony in England averaged 15.64 g day-1 (range 15.07 g day^{-1} - 16.21 g day^{-1}) in 1954-1957. Kittiwake chicks on the Fame Islands gained about 15 g day^{-1} (Pearson 1968) and chicks on the east Murman coast in northern Russia gained about 12 g day^{-1} (Belopolski 1957).

Table 6 lists mean volumes of kittiwake eggs measured at Bluff, Cape Thompson and Cape Lisburne. The mean value of all categories, 48.7 mm^3, is larger than volumes of eggs laid by kittiwakes at the same latitudes in the North Atlantic Ocean (see Runde and Barrett 1981). Eggs in two-egg clutches were larger than eggs in one egg clutches in 1977 and 1981 and the difference was significant in 1977 (t = 2.95, P < 0.05). Eggs in one-egg clutches were significantly larger (t = 2.04, P < 0.05) at Cape Thompson in 1979 than in 1977.

VIIc. KITTIWAKES - DISCUSSION

The consistent pattern of change in elements of the breeding biology of black-legged kittiwakes at colonies in northern Alaska suggests that birds nesting in a large geographic area were similarly affected by a change or changes in the environment. Indeed, a close association between variation in the physical environment and estimates of kittiwake breeding phenology and productivity is apparent in Figure 5. Belopolski (1957)

described similar relationships between kittiwake reproductive success and breeding phenology and environmental change in the Barents Sea. He also said that changes in kittiwake food availability, which were associated with regional changes in water temperatures accounted for the annual differences he saw in the breeding biology of the birds.

The importance of food availability to the timing of breeding seasons and levels of reproductive success has been reviewed by Perrins (1970) for several species of terrestrial and marine birds. The pattern of change we saw in the breeding biology of kittiwakes in northern Alaska during recent years suggests that annual change in food availability was the ultimate factor affecting kittiwake breeding phenology and reproductive success.

Food habits studies of thick-billed murres, common murres and black-legged kittiwakes at Cape Thompson and Cape Lisburne revealed important annual and seasonal differences in foods used by all three species between 1976 and 1980 (see sections V. b. - VII. b.). In general, fish biomass was low in 1976 but rose steadily during later years, largely as a result of increased stocks of sand lance in particular, and capelin to a lesser extent. Changes in food availability were associated with the warming trend shown in Figure 5. Adult murres and kittiwakes ate more sand lance earlier each year between 1977 and 1979. Sand lance were apparently unavailable to kittiwakes throughout 1976. Less is known about the food habits of kittiwakes at Bluff or St. Lawrence Island, but sand lance are also important at these colonies (Drury *et al.* 1981, Springer *et* al. unpubl. data).

Early laying dates and apparently high levels of egg production by kittiwakes in *1980* and 1981, but greater chick mortality and slower growth rates than in 1979, indicate a failure of the food supply mid-way through both breeding seasons. In 1980 at Cape Lisburne, kittiwake chick diets, on a wet weight basis, consisted of about 31% sand lance, 20% capelin, 20% cod and sculpins, 28% euphausiids, and 1% other fish and invertebrates (Springer *et al.* unpubl. data). Sand lance was essentially the only food given to kittiwake chicks in all earlier years when chick mortality was relatively low and growth rates were high.

The importance of sand lance to kittiwake chick growth is also apparent from our observat.ions in 1977. In that year chicks hatched earlier at Cape Thompson than at Cape Lisburne; however, sand lance schools arrived earlier at Cape Lisburne, at about the same time that the chicks hatched. They did not arrive in large numbers at Cape Thompson until about 10-14 days after chicks hatched there. The abnormally low rate of growth at Cape Thompson in 1977 was probably due to the lack of sand lance, or suitable alternative, until well after the chicks had hatched.

Arctic cod also contribute significantly to the diet of kittiwakes in the eastern Chukchi Sea. However, Arctic cod are demersal fish and are probably never as abundant, relative to the kittiwake's ability to catch them, as are sand lance and capelin, which form dense schools near the surface. Therefore, the contribution of sand lance and capelin to

exploitable fish biomass may be the necessary ingredient for kittiwakes to enjoy successful reproductive seasons in northern Alaska.

The differences in annual trends of breeding phenology and reproductive success between northern kittiwake populations and those that breed on the Pribilof Islands--variable versus stable--can probably be explained by the different food webs that support kittiwakes in the two regions. The Pribilof Islands lie in the open ocean in relatively deep water near the continental shelf break. Kittiwakes on the Pribilof Islands depend on walleye pollock (Hunt et al. 1981), the dominant fish species in the stable pelagic food web of the outer shelf zone of the southeastern Bering Sea (Iverson et al. 1979). Relatively stable prey populations should result in uniform dates of breeding activities, levels of reproductive success and chick growth rates. Neither growth rates nor reproductive success would be particularly high because pollock, like Arctic cod, are generally found in water deeper than kittiwakes can exploit, and occur in less consolidated schools than do sand lance and capelin. Thus, while providing a uniform level of energy, this level is probably seldom, if ever, as high as at colonies where sand lance and capelin occur in large numbers.

Although we still lack many details concerning the relationships of kittiwakes to their food webs in northern Alaska, it is clear that available fish biomass varies considerably between years, probably in response to changing climatic conditions which affect the regional marine environment. Kittiwake productivity consequently fluctuates between very low and very high levels, but over the long-term, numbers of chicks produced per breeding pair are probably similar to numbers produced at more stable colonies such as those on the Pribilof Islands. In the years 1976-1979, 100 pairs of kittiwakes on the Pribilof Islands would have produced about 185 chicks. One hundred pairs of kittiwakes would have produced about 204 chicks at Bluff, 218 chicks at Cape Thompson and 246 chicks at Cape Lisburne during the same interval. These higher overall levels of productivity would tend to offset the counter effect of fewer breeding attempts in years when reproductive success *was low,* and result in levels of production for the northern populations that would be about the same as for the Pribilof Islands population. Therefore northern kittiwake populations are probably maintaining themselves without relying on immigration of birds from outside of the region.

Because natural variation in reproductive success is high in kittiwake populations in northern Alaska, additional effects of resource development could be devastating. In Peru, the combination of El Nino events and commercial fishing led to a decline in the number of guano birds from 28 million to about 5 million during the 1950's and 1960's (Shaeffer 1970). The effects of commercial fishing in Alaska may already threaten certain seabird populations (see sections V. a - VII. a.). Since stocks of the more commercially valuable fishes worldwide are already heavily fished, further increases in catches will depend on the development of fisheries that target less preferred species (Gulland 1978) . Capelin and sand lance are both receiving greater attention in Alaska as possibilities for expansion of the State's commercial fishing industry (Warner 1981, R. Wolotire pers. comm.). Increased interest in

these species is a cause for concern for the maintenance of trophic systems that may be critical to the success of kittiwake populations in northern Alaska.

Vd. OTHER SPECIES - METHODS

In addition to murres and black-legged kittiwakes, pelagic cormorants *(Phalacrocorax pelagicus)*, glaucous gulls *(Larus hyperboreus)*, black guillemots *(Cepphus grylle)*, pigeon guillemots (C. *columba)*, horned puffins *(Fratercula corniculata)*, and tufted puffins *(Lunda cirrhata)* breed at colonies in the eastern Chukchi Sea. Numbers of all of these species were small by comparison to numbers of murres and black-legged kittiwakes, and nest sites of those that bred were generally inaccessible. For these reasons, and because we saw little change in their numbers or reproductive success at Cape Thompson in 1976-1979 compared to observations made by Swartz (1966), we devoted relatively little time to them.

We censused all six breeding species in at least one year at Cape Thompson and we recorded information on reproductive success of cormorants and gulls in one or more years at Cape Thompson and Cape Lisburne. We made numerous observations-of-opportunity throughout the study. Selected data are compared to similar data reported by Swartz (1966), who made more thorough studies of most of these species at Cape Thompson in 1960. Summary information is presented in following discussions, and additional information and details are presented in previous annual reports.

Eiders *(Somateria spectabilis* and S. *mollissima)* were also common throughout the summer in Ledyard Bay, especially as they passed by Cape Lisburne during migration. We have included observations of these water-fowl because the region appears to be important to them, particularly in August as they move south out of arctic nesting areas.

VId. - VIId. OTHER SPECIES - RESULTS AND DISCUSSION

Pelagic Cormorants

Numbers of pelagic cormorants at Cape Thompson have been variable. Numbers have fluctuated between years, especially at Colony 1 and Colony 2, but show no consistent trend (Table 1). The greatest change occurred at Colony 2. The marked difference in nesting pairs between 1959 and 1960 may have been due, in part, to less survey effort. Surveys for species other than murres and kittiwakes were less complete in 1959 than in 1960 or 1961 (Swartz, pers. comm.).

In 1960 and 1961, most of the cormorants at Colony 2 nested at one location (Swartz unpubl. data). Most of that section of cliff had sheared off since the time of Swartz's (1966) study, and the loss of that nesting area may account for much of the difference between 1959-1961 and 1976-1978.

Whereas the total number of nesting pairs of cormorants varied from 11 to 18 in 1976-1978, productivity remained relatively stable. Ten nests contained 2.2 large chicks nest^{-1} on 16 August 1976, and 11 nests

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TABLE 1. Black-legged kittiwake census summaries for colonies in northern Alaska, 1975-1981.

Colony	1975	1976	1977	1978	1979	1980	1981
Bluff[a]	7,250	7,000	7,400	6.600	9,000	9,900	10,700
Cape Thompson	ND[b]	10,500	10,200	15,200[c]	16,800	ND	ND
Cape Lewis	ND	ND	2,300	5,800[d]	ND	ND	5,200
Cape Lisburne	ND	ND	14,700	15,400[e]	17,300[e]	ND	16,300[e]

[a] Data for 1975-1976 are from Steele and Drury (1977); data for 1977 are from Biderman et al. (1978); data for 1978 are from Ramsdell and Drury (1979).

[b] ND = no data.

[c] Estimate derived from the count of Colony 4 only. The value is the mean (S=1900) of three estimates of the 1978 colony total. The estimates were derived by using each of the other three years as bases for extrapolating the colony total from counts at Colony 4 in 1978.

[d] Estimate derived from a count of 50% of the census plots. The value is the mean (S=380) of two estimates of the 1978 colony total. The estimates were derived by using each of the other two years as bases for extrapolating the colony total from partial counts in 1978.

[e] Estimate derived from counts of selected census plots within the colony.

TABLE 2. Black-legged kittiwake nest count summaries at Cape Thompson, Alaska.[1]

Colony	1960	1961	1978	1979
1	0	0	0	0
2	5,200	ND[2]	ND	4,600
3	2,600	ND		3,700
4	3,100	3,000	1::00	2,800
5	3,200	ND	ND	2,500
Total	14,100			13,500

[1] Data from 1960 and 1961 are from Swartz (1966).

[2] ND = no data.

TABLE 3.   Results of Multiple Comparison Procedure (Conover 1980) comparing growth rates (lower left) and hatching phenology (upper right).   Significant differences between sample means (P < 0.05) indicated by +; no significant difference indicated by O.

		Bluff				Cape Thompson		Cape Lisburne					St. Law. I.
		1978	1979	1980	1981	1977	1979	1977	1978	1979	1980	1981	1981
Bluff	1978		+	+	+	+	+	+	+	O	+	+	0
	1979	O		O	O	+	+	+	+		+	+	+
	1980	O	+		0	+	+	+	+	+	+	+	+
	1981	+	+	O		+	+	+	+	+	+	+	+
Cape Thompson	977	+	+	+	+		+	+	O	+	+	+	+
	979	+	o	+	+	+		+	+	+	+	+	+
Cape Lisburne	977	O	O	+	+	+	o		+	+	+	+	+
	1978	O	O	+	+	+	O	O		+	+	+	+
	1979	O	O	O	+	+	o	O	O		+	+	o
	1980	O	+	O	+	+	+	+	O	O		0	+
	1981	+	+	+	0	0	+	+	+	+	+		+
St. Lawrence I.	1981	0	0	0	+	+	0	0	0	0	0	0	

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TABLE 4. Black-legged kittiwake clutch size per completed clutch at colonies in northern Alaska.[1]

Colony	Year								
	1960	1961	1975	1976	1977	1978	1979[1]	1980	1981
St. Lawrence I.[2]	1.[2]	–	–	–	1.0	–	–	–	1.61
Bluff[3]			1.22	1.11	1.08	1.56	1.45	1.45	1.72
Cape Thompson[4]	1.92	1.88	–	1.12	1.18	–	1.58	–	–
Cape Lewis				–	1.17	–	1.64	–	–
Cape Lisburne				1.0	1.14	1.23	1.80	1.61	1.67
St. Paul I.[5]			1.42	1.49	1.52	1.33	1.47	–	–
St. George[5]	1.[5]	–	–	–	1.42	1.46	1.20	–	–

[1]Values for St. Lawrence I. in 1981, Bluff in 1979-1981, Cape Thompson in 1976, Cape Lewis in 1977 and 1979, and Cape Lisburne in 1976-1978 and 1980-1981 are nest contents on our first visit. First visits at those colonies in those years occurred approximately when eggs were hatching so the values reported represent minimum estimates of actual clutch sizes.

[2]Data for 1976 are from Searing (1977).

[3]Data for 1975-1978 are from Drury et al. (1981).

[4]Data for 1960-1961 are from Swartz (1966).

[5]Data are from Hunt et al. (1981).

TABLE 5. Growth rates of black-legged kittiwake chicks in northern Alaska.

Year	Colony			
	Bluff	Cape Thompson	Cape Lisburne	St. Lawrence I.
1977	ND[a]	12.6 ± 3.6 (16)[b]	19.3 ± 2.9 (18)	ND
1978	17.9 ± 4.1 (22)	ND	19.7 ± 6.7 (21)	ND
1979	20.4 ± 4.4 (35)	20.2 ± 4.7 (111)	18.3 ± 1.4 (24)	ND
1980	17.6 ± 7.4 (30)	ND	17.9 ± 3.7 (43)	ND
1981	15.6 *4.5 (31)	ND	14.3 ± 3.0 (30)	21.0 ± 7.1 (15)

[a]ND = no data.

[b]Mean growth rate (g day^{-1}) ± standard deviation (sample size).

TABLE 6. Black-legged kittiwake egg volumes at colonies in northern Alaska.

Colony	Clutch/Size	Year 1977	1979	1981
Bluff	1 egg	ND[a]	ND	47.9 ± 2.0 (7)[b]
	2 eggs	ND	ND	48.9 ± 3.3 (55)
Cape Thompson	1 egg	45.1 ± 3.1 (19)	47.3 ± 4.3 (44)	ND
	2 eggs	46.9 ± 1.8 (6)	47.1 ± 3.5 (142)	ND
Cape Lisburne	1 egg	ND	ND	47.3 ± 3.0 (27)
	2 eggs	ND	ND	48.4 ± 3.5 (86)

[a]ND = no data.

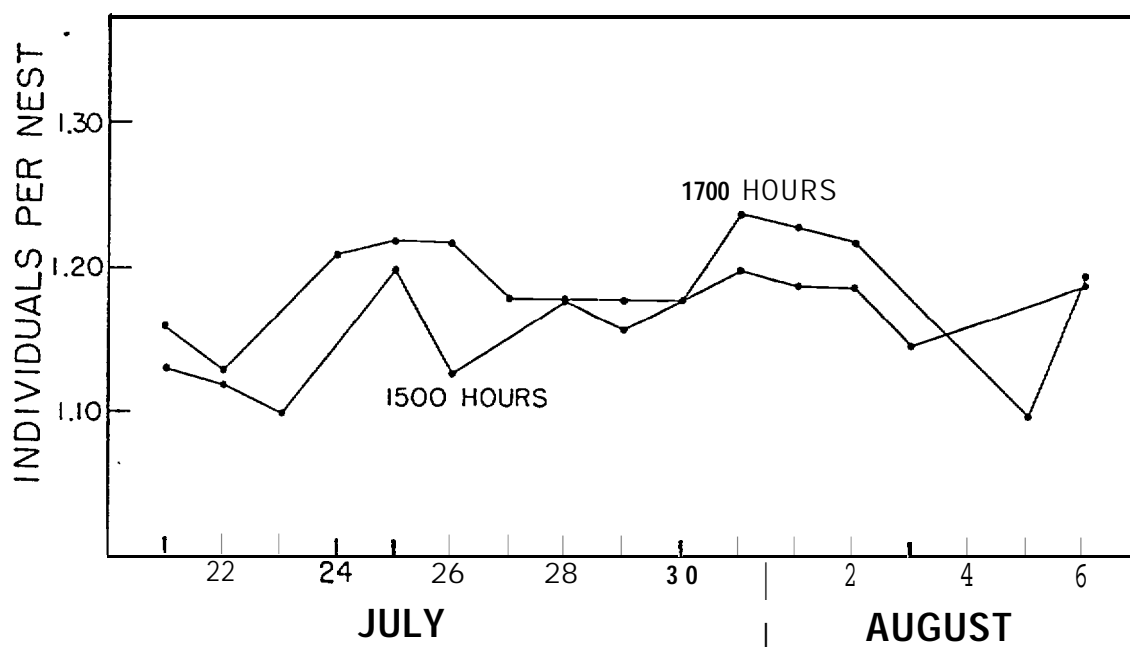[b]Mean volume $(mm^3) \pm$ standard deviation (sample size).

Figure 1. Daily variation in kittiwake numbers during the nestling period at Bluff in 1979.
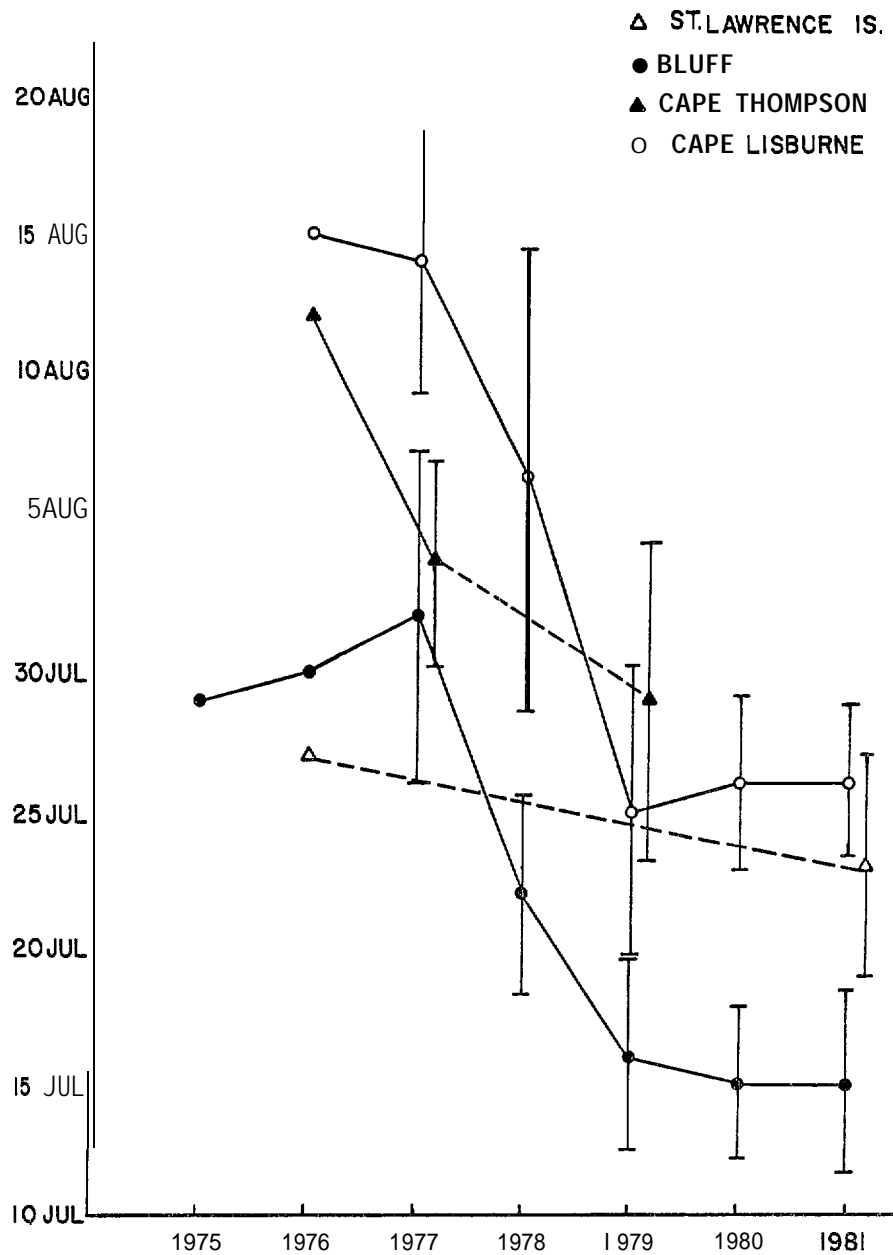
Figure 2. Mean hatching dates of kittiwake chicks. Dates
for 1975-1977 are from Drury *et al.* (1981); date
for 1976 at St. Lawrence Island was estimated
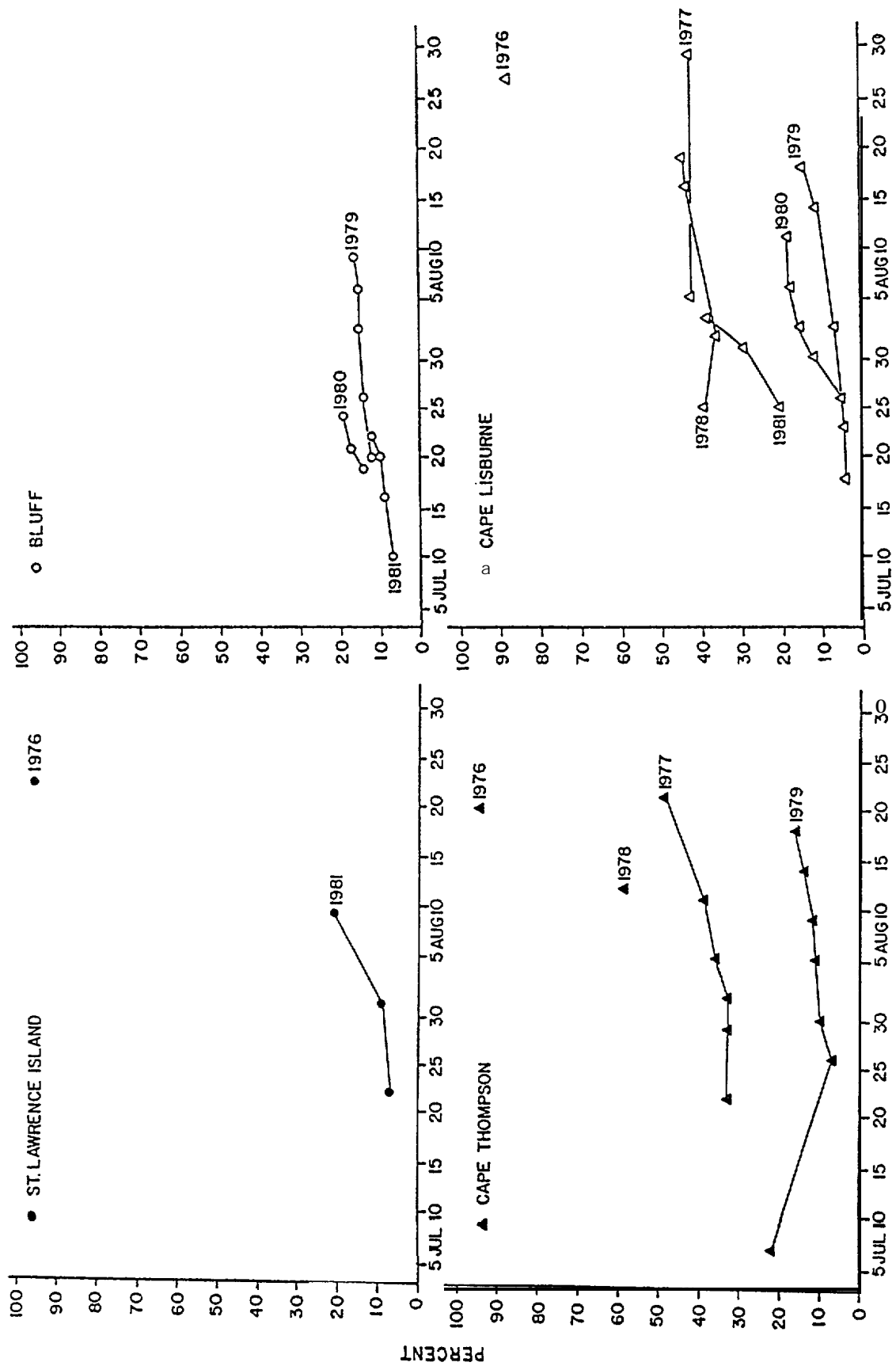from data reported by Searing (1977).

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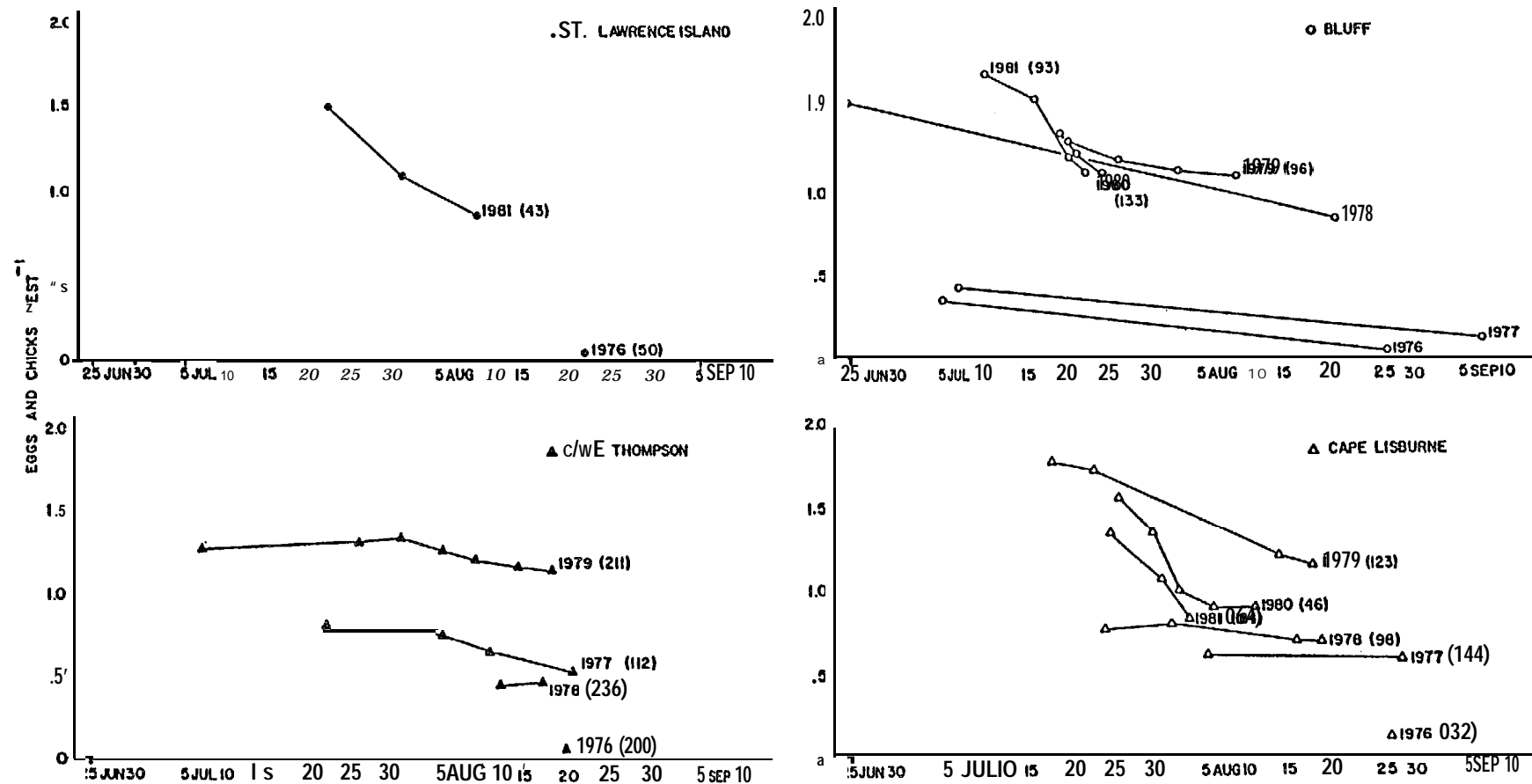Figure 3. Percentage of empty kittiwake nests at colonies in northern Alaska.

Figure 4. Mean number of kittiwake eggs and chicks per nesting attempt. Data for Bluff in 1976-1978 are from Drury *et al.* (1981); datum for St. Lawrence Island in 1976 is from Searing (1977). Sample size is in parentheses.
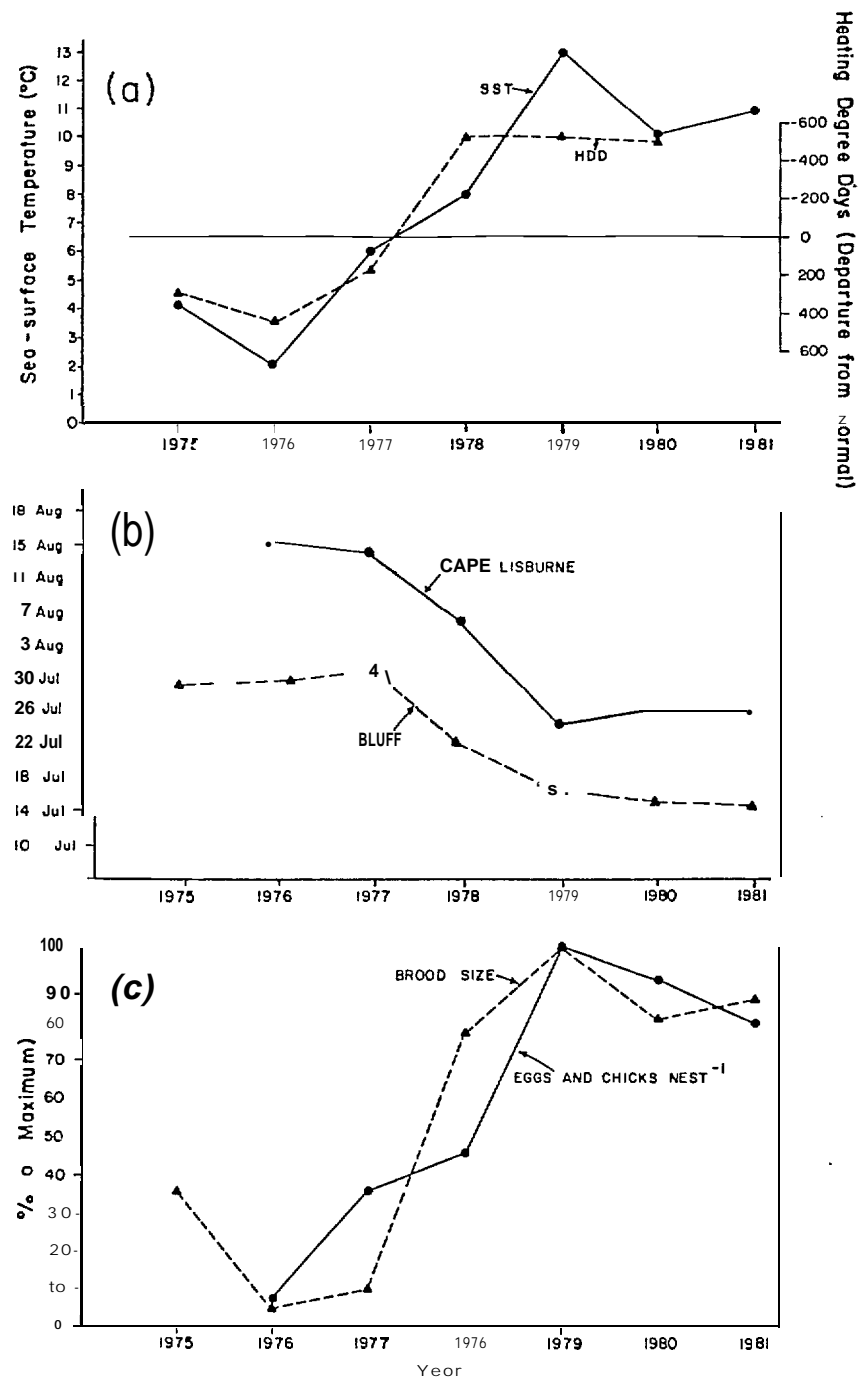
Figure 5. Relationships between environmental change, kittiwake nesting phenology and estimates of kittiwake reproductive success at Cape Lisburne and Bluff. (a), (b), and (c) as in Figure 21, page 77.

contained 2.3 large chicks nest[-1] on the same date in 1978. We saw the contents of only 2 nests on 23 August 1977, and although the sample size was small, the brood size of 2.5 large chicks nest^{-1} was similar to that found in both 1976 and 1978.

Total cormorant nests declined from 39 in 1977 to 25 in 1978 at Cape Lisburne. Average brood size at the 25 nests examined on 17 August 1978, 2.6 large chicks nest^{-1}, was considerably higher than the average brood size of 2.0 large chicks nest^{-1} at 36 of the 39 nests examined on 20 August 1977.

Numbers of cormorants at Cape Lewis increased from 28 nesting pairs in 1977 to 53 nesting pairs in 1979. Although it was difficult to determine nest contents at Cape Lewis, it appeared that the majority of the 53 nests contained three young each on 21 July 1979.

Cormorants do not nest at Corwin Bluff, about 40 km east of Cape Lisburne, but large numbers of non-breeders appear to roost there. Numbers of non-breeding birds increased steadily from 33 in 1977 to 53 in 1979 to 79 in 1980. Increases in 1979 and 1980 may have been the result of relatively good reproductive success at Cape Lisburne and Cape Lewis in 1978 and 1979. They might have also resulted from improving feeding conditions in Ledyard Bay following 1976. These increases are similar to annual increases of glaucous gulls in Ledyard Bay between 1977 and 1979.

Eiders

Large flocks of king and common eiders, generally composed of 100-500 birds, were commonly seen migrating from east to west along the northern coast of the Lisburne Peninsula each year. We first noted these migrations at Cape Lisburne in late August and early September 1976, and obtained some additional information on eiders in following years.

On 25 July 1978, while flying an aerial survey of birds in Ledyard Bay, 35 flocks of eiders were observed on the water. Flocks varied in size from about 100-400 birds. One observer estimated that these flocks totaled about 12,000 individuals, and a second observer estimated that 12,000-15,000 individuals were present. Several other flocks, varying in size from 12 to several hundred birds were also seen during the survey.

Most of the eiders were found along a 50 km section of a transect line running almost directly between Point Lay and Cape Lisburne, and the heaviest concentration occurred within a 20 km subsection near the center of the transect (see Springer *et* al. 1979). Two days later on 27 July, large numbers of eiders were seen offshore between Ayugatak Lagoon and Corwin Bluff, and by 31 July large skeins of birds were migrating westward past Cape Lisburne. Flocks of about 200 birds each passed the Cape regularly on 2 August, and on 15 August migrating flocks were seen continuously along the coast as far east as Corwin Bluff.

Eiders also migrated west along the coast of Ledyard Bay in 1979. On 17 August during a short boat trip east of Cape Lisburne, we saw four

flocks totaling about 750 common eiders about 8 km west of Ayugatak Lagoon. Three of the flocks were flying west and one was resting on the water.

Five-minute counts at Cape Lisburne in late July 1980 (Table 6) indicated the size and pattern of these annual migrations. We estimated that in the order of 50,000 individuals may have passed the Cape each day during 27-31 July that year, based on the average number of birds (464 ± 538 per 5 minute interval) observed between 1400 h and 2300 h.

We know little about the route taken by eiders after they pass Cape Lisburne, but it is clear that they remain well offshore after rounding the Cape. Southward migrations were not evident at Noyalik Peak or Cape Lewis, nor were they evident at Cape Thompson during late summer 1976-1979, a location where notable spring and early summer migrations occur (see Williamson *et* al. 1966).

The late summer molt migration of eiders is relatively well documented (e.g., Bent 1925, Thompson and Pearson 1963, Johnson *et al.* 1975), and most accounts of it are similar. From about early July to early August, flocks of male common and king eiders begin to move westward along the Beaufort Sea coast from breeding grounds in Alaska and Canada (see also Harrison 1977). Flocks of hundreds of individuals have passed given points every few minutes, especially during favorable wind conditions. Approximately 18,000 birds (mostly king eiders) passed over Point Barrow every day between 14 July and 1 September 1953 (Thompson and Pearson 1963). Until 8 August the majority of birds were males (about 22:1), but during the period 8-17 August, the sex ratio shifted to a preponderance of females. Although the largest flock contained 1,100 birds, mean flock size was 105 birds.

Major westward movements of eiders have also been recorded on radar during the last week in July and the first week in August at several locations in northern Alaska (Flock 1973). After eiders pass Point Barrow, they tend to follow the coast at distances of 1.5 km or more off shore at least as far as Point Lay.

Common and king eiders apparently molt in the vicinities of Icy Cape and Point Lay (see Thompson and Pearson 1963, Johnson et al. 1975). Most of the eiders seen concentrated in Ledyard Bay on 25 July 1978 were in less than full breeding plumage. Many may have been flightless since most swam from the path of the approaching aircraft.

It is also possible that eiders stage in Ledyard Bay before migrating on to their wintering grounds. Murres and kittiwakes feed extensively in the bay, and perhaps eiders, too, find the shallow waters a productive area in which to feed before resuming their southward journey.

Glaucous Gulls

Glaucous gulls were censused at Cape Thompson in 1976, 1977 and 1979. In 1976, 144 nests, the equivalent of 288 adults were counted at Colonies 1-4; neither nests nor adults were counted at Colony 5. Swartz

(1966) reported that the population at all five colonies was 304 and 300 adult gulls in 1960 and 1961, respectively. Fourteen adults were found at Colony 5 in 1960 and 28 were present in 1961. Swartz's totals for Colonies 1-4 for 1960 and 1961, 290 and 268 adults, respectively, were similar to our projected total of 288 adult glaucous gulls in 1976.

In 1977, we counted 250 adult glaucous gulls at all five colonies at Cape Thompson on 20-21 August. Most gull chicks had already fledged and some had moved a short distance from the colonies. An additional 39-50 adults with juveniles were counted along nearby upcoast and downcoast beaches, bringing the total adult population to 289-300, a figure close to the totals for all previous years.

Adult glaucous gulls were censused again at Cape Thompson on 16 August 1979. The total number, 386, was considerably greater than in any other year. The change was similar to changes we observed in numbers of breeding black-legged kittiwakes between 1976 and 1979.

The population of glaucous gulls at Cape Lisburne is smaller than the population at Cape Thompson. In 1976 we estimated that 100-200 individuals were present at or near the colony during 26-29 August; no distinction was made between adults, subadults and juveniles. In 1977 it was clear that, at most, only about 50 adults regularly occupied the Cape Lisburne colony. We only found two nests in 1977, but several other widely scattered pairs were seen along the cliff-tops at typical, grassy nesting areas where they might have been attending nests. The 1976 estimate of total numbers was probably inflated by the presence of subadults, which typically appear in greater numbers at both Cape Thompson and Cape Lisburne after late July-early August. Although counts of adult glaucous gulls were not made in 1978-1981 at Cape Lisburne, numbers did not appear to change relative to 1977.

Estimates of glaucous gull productivity were made only at Cape Thompson. We examined a total of 29 nests at colonies 1 and 4 on 28 June and 4 July, respectively. The nests contained a total of 34 eggs and 24 chicks, or 2.0 eggs and chicks nest-1. Swartz (1966) reported a mean clutch size of 2.86 in 1960. If egg counts had been made earlier in the season in 1976, the difference between our data and those of Swartz would probably have been less, since some eggs were probably lost during incubation.

Nineteen nests were checked at Colony 1 on 16 July and 21 nests were checked there on 4 August 1976. Brood size fell to 1.9 chicks nest-1 during the first interval and to 1.4 chicks nest^{-1} during the second interval. No chicks had fledged by 4 August so brood size on that date does not necessarily represent fledging success.

Estimates of reproductive success were not made at Cape Thompson in 1977 or in 1979. Counts of adults and juvenile gulls in mid-late August of both years indicated that productivity was similar to productivity in 1976. We counted all gulls in the vicinity of Cape Thompson on 20 August 1977 and on 16 August in 1979. In 1977 we obtained a ratio of 0.63 juveniles per adult, or 1.26 juveniles per projected pair, and in

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1979 we obtained a ratio of 0.41 juveniles per adult, or 0.82 juveniles per projected pair.

We obtained phonological information on glaucous gulls in 1976 and 1977 at Cape Thompson, and in 1977 at Cape Lisburne. Breeding schedules at Cape Thompson were similar in 1977 and 1959-1961 (see Swartz 1966), but about 10-15 days later in 1976. Only 13 of 33 eggs had hatched by 28 June 1976. In 1977 at Colony 1 adults were incubating on 8 June, and most eggs had hatched before about 1 July. Hatching was essentially complete by 6 July. Although two small downy chicks (∿ 70 g each) were only about 3-5 days old on 7 July, most chicks were relatively large by early July. Seven large, well-feathered young were present at Colony 3 on 15 July, and some juveniles were capable of flight a few days later. Many juveniles were flying by the first week of August, and almost all of the chicks had fledged by 15-20 August.

In 1977, glaucous gulls may have bred about 10 days later at Cape Lisburne than at Cape Thompson, and may have followed a schedule similar to that followed at Cape Thompson in 1976; however, our data are from only two nests. The two nests contained five chicks estimated to be about 10 days old on 14 July.

The proportion of subadult to adult glaucous gulls at Cape Thompson and Cape Lisburne increased greatly between 1976 and 1979, and subadult gulls were seen earlier each summer after 1977. In 1976 subadult glaucous gulls were not observed at the Cape Thompson colonies until 1 August. Of 164 gulls in the immediate vicinity of the colonies on 20 August, only 7% were subadults.

In 1977 subadults again appeared at both Cape Thompson and Cape Lisburne during the first few days of August. By 20-21 August they accounted for about 6% of the total 440 gulls observed at Cape Thompson. Of an additional 127-152 gulls located farther away from the colonies upcoast and downcoast along the beaches, 31-33% were subadults. Area wide, subadults accounted for 17% of the 567-593 gulls counted on 20-21 August .

On 2 August 1977 at Cape Lisburne, 12 subadults (13%) were identified among 89 glaucous gulls counted between the colony and Thetis Creek. By 15 August subadults had become somewhat more numerous and were observed near the colony; however, no counts were made of the relative number of adults and subadults.

Data on subadult glaucous gulls were gathered on 29 July 1978 during a flight from Cape Thompson to Point Hope. Approximately 250 gulls were counted along the shoreline and about 25% of these birds were subadults. On a 17 September flight from Cape Thompson to Krusenstern Lagoon, 216 glaucous gulls were counted and aged and 43% were subadults. Groups totaling about 75 additional gulls were also seen during this flight and about 50-75% were estimated to be subadults.

The earliest counts of glaucous gulls in the Cape Lisburne vicinity in 1978 were made during an aerial survey flight on 25 July, but sub-

adults were already present at Cape Lisburne when we arrived on 22 July. Three flocks of about 75 gulls each were seen along the lagoons approximately 9-16 km east of Cape Lisburne; about 10% of these birds were subadults. Two days later on 27 July, 1,150 gulls were counted along the coast from a point about 35 km south of Point Lay to Wainwright. We classified 767 of these birds and 168 (22%) were subadults; however, the distribution of subadult gulls was not uniform. From the starting point south of Point Lay to Icy Cape, 9% of 487 birds were subadults, but between Icy Cape and Wainwright 44% of 280 individuals were subadults.

Glaucous gulls were also counted during several boat trips east from Cape Lisburne in 1978. On 29 July 200 gulls were seen between Cape Lisburne and Corwin Bluff, of which 10-15% were subadults, a ratio consistent with the aerial data from south of Icy Cape. Several weeks later, on 15 August, major changes had occurred in the numbers of gulls and in the proportion of adults to subadults. Within 20 km to the east of Cape Lisburne we counted six flocks of gulls and kittiwakes, each comprised of 750-1,000 birds. Each mixed flock contained between 100 and 350 glaucous gulls, or about 1,000 gulls total. Aging the birds was difficult, however, our best estimate suggested that about 90% were subadults.

We also gathered some data on gulls between Cape Lisburne and Corwin Bluff in 1979. On 20 July about 200 gulls were counted on the lagoons 9-16 km east of Cape Lisburne and about half (50-60%) were subadults. On 17 August three flocks of 25 birds each were observed near the lagoons and at least 125 additional gulls in flocks of 5-50 birds each were counted flying west between the lagoons and Corwin Bluff. On our return trip, 300-400 gulls (presumably the same birds observed in smaller flocks earlier in the day) were counted at Ayugatak Lagoon. About 80-90% of all glaucous gulls observed on 17 August were subadults.

Little information was gathered on subadult glaucous gulls at Cape Thompson in 1979. However, subadults were observed flying in the vicinity of the colonies upon our arrival on 2 July, much earlier than in previous years. We did not actively look for subadults again until 17 July when we began seeing them in larger numbers. On 21 August, 343 glaucous gulls were classified as to age between Ogotoruk Creek and Kivalina during a flight to Kotzebue, and of these, 15% were subadults.

The changes observed in total numbers of glaucous gulls at Cape Thompson and Cape Lisburne were due primarily to an increase in the subadult component of the population. Subadult gulls were observed near the colonies much earlier each year after 1978. No subadults were seen at Cape Thompson in June of 1976 or in July of 1976 and 1977, nor were subadult gulls seen at Cape Lisburne during July of 1977. In both 1976 and 1977, subadults began arriving at Cape Thompson and Cape Lisburne in August. Subadults arrived at both colonies somewhat earlier in 1978 and 1979.

After subadult gulls began arriving, they continued to increase in numbers at both colonies throughout the remainder of the season each year, and constituted progressively greater and greater proportions of the total

populations. An age structure developed solely on data obtained at Cape Lisburne in 1978 would have suggested that only 10-15% of all gulls within the region were **subadults;** however, by late August subadults not only accounted for about 90% of all gulls, but the total population was about an order of magnitude greater than it had been in July. Therefore, we suggest that numbers data be used cautiously in forming conclusions regarding changes in the size or age structure of glaucous gull populations in the **Chukchi** Sea since widely different results may be obtained, depending upon census dates.

We question whether the major changes in numbers of **subadult** glaucous **gulls** represent either recent (i.e., during the past 5 years) changes in gull productivity, or major changes in gull survivorship. A flock of subadult gulls could be composed of one, two and three year-old birds. Many of the birds in the flocks we saw at Cape **Lisburne** in 1978 were certainly alive in the previous 1-2 years, and may have summered offshore or in some other region. We believe subadult gulls may have occurred in the vicinity of Cape Lisburne in large numbers in 1978 as a result of early, bountiful supplies of forage fish, particularly sand lance. Except for a few breeding birds, all of the gulls were found east of the Cape Lisburne colony and were feeding, perhaps exclusively, on these. fish'.

The changes we have seen in the glaucous gull population at Cape Thompson and Cape Lisburne over the years are consistent with changes we have observed in other species of seabirds. We believe the causative factors underlying these changes are the same. The prey base upon which the birds depend recovered steadily between 1977 and 1979 from a low in 1976, and has remained relatively stable since then. Food subsidies for gulls, particularly at garbage dumps, may also be responsible for increases in gull populations; however, we stress that conclusions regarding the effects of these and similar sources of food on populations of northern gulls be arrived at carefully, keeping in mind parallel changes in other elements of the ecosystem.

Black Guillemots

One noteworthy event at Cape Lisburne was the discovery of a large population of black guillemots (Table 2). During a brief survey in late August 1976, fewer than ten black guillemots were found there, but in 1977 black guillemots were relatively numerous when we arrived on 6 **July,** and a minimum of 136-151 individuals were regularly observed at the colony from mid-July through early August. Groups of 30-40 birds commonly perched on or near the same boulder piles where most of the 1976 sightings had occurred, but after a severe storm on 8-9 August only a few pairs remained in the area. These few pairs may have been the only ones that nested successfully that year.

On 9 and 10 July 1978, 9-11 black guillemots were observed on the water in front of the cliffs on the north side of the colony. These few birds were probably not representative of the actual number present on that date because the west side of the colony was not surveyed until two weeks later. On 24 July 108 black guillemots were counted within the colony boundaries.

Conditions in 1979 did -not provide an opportunity to conduct a complete census of black guillemots at Cape Lisburne. Nevertheless, approximately 50 birds were regularly observed between mid-July and mid-August on or near the beach at the east end of the colony.

Two complete counts of black guillemots at Cape Lisburne in 1980 indicated that a minimum of 126-154 birds were present at the colony that year, at least during early to mid-August. These numbers are similar to those obtained in 1977 when black guillemots were also censused more than once.

Counts of black guillemots were not as high in 1978 and 1979 as they were in 1977 and 1980; however, less effort was made to count them in 1978 and 1979. We believe that comparable census efforts would have' provided comparable results among all four years.

Observations of black guillemots from the vicinity of Cape Lisburne, but outside of the colony boundaries, were also made in 1977-1980. In 1977, 14 birds were found frequenting the coast between Kay Creek, near the colonie's southern boundary, and Noyalik Peak, and 24 additional birds were present at Cape Lewis. Although we did not count guillemots at Cape Lewis in 1978, some were present, and we found 46 individuals in the section of coast between Kay Creek and Noyalik Peak. Black guillemots were also regularly seen along the northern coast east to Corwin Bluff. In 1977, our highest count in that section was nine individuals, and numbers seemed comparable in 1978. A minimum of 56 individuals was present there in 1980.

Cape Thompson appears to represent the southernmost breeding location of black guillemots in Alaska. Although some individuals have been seen occasionally at colonies farther south in and near Bering Strait, nesting pairs have apparently never been documented at them.

The population of black guillemots at Cape Thompson has been consistently small and variable since 1959 (Table 3), and only one nest has been located there. Swartz (1966) found a nest containing two eggs in a crevice several feet above a talus slope in 1960. He collected one egg and found the second egg broken and deserted the next time he checked the nest.

We have found evidence of breeding by black guillemots at Cape Lisburne. A dead 14-21 day-old chick was discovered at the base of a large boulder pile on 26 August 1976. Two nests were located in 1977. One contained two eggs on 12 July, but both eggs were found broken on 5 August. One of the eggs contained the remains of a well-developed chick. A second nest only a few meters from the first was repeatedly entered by an adult carrying fish on 25 July; however, the nest contents and fate are unknown. In 1978 a nest under a split boulder had one egg in it on 11 July, and another nest containing a single egg was eventually located in a crevice on 2 August 1980.

We are uncertain as to how many black guillemots actually breed at Cape Lisburne, and we are also unsure of their breeding success. Of the

four known nests at Cape Lisburne, one failed and fates of the other three are unknown. At least two of the nests contained single eggs, whereas two-egg clutches are more typical (see Bent 1919). Divoky (1978) reported an average clutch size of between 1.75 and 1.95 in 1975-1977 at Cooper Island. However, overall breeding success of black guillemots at Cooper Island dropped dramatically in 1976 and 1977 after near perfect success in 1975. Divoky attributed the decline to increased predation by Arctic foxes and an increase in the number of inexperienced breeding pairs at new nest sites. Nests used for the first time had smaller average clutch sizes and breeding success was poorer at these nests than at nests used in previous years.

We have observed black guillemots regularly flying in and out of inaccessible cracks and crevices high on the cliffs in a variety of locations where quality of nesting habitat appears superior to the storm-lashed bases of the cliffs. At least some of the nests we found at Cape Lisburne may have been those of inexperienced pairs as indicated by their placement at the bases of the cliffs, and single-egg clutches.

East of Cape Lisburne black guillemots were often observed flying off of dirt bluffs where they may also nest (see Asbirk 1978), and some pairs probably breed along the bluffs and cliffs south of Cape Lisburne and at Cape Lewis. The full extent to which Cape Lisburne and vicinity are used for nesting is still unknown.

We have some information on prey taken by black guillemots at Cape Lisburne. Fourteen observations of birds carrying fish into boulder piles were obtained during 22-25 July 1977. In one case the fish was a sand lance, but in 12 cases the fish were clearly small cod, and in one case the fish was clearly an Arctic cod. Arctic cod were numerous under the ice floes that remained near the colony at the time these observations were made, and most, if not all, of the cod were probably of that species. Divoky *et al.* (1974) reported that Arctic cod were fed to chicks in the Beaufort Sea.

Pigeon Guillemots

A small and variable population of pigeon guillemots inhabits Cape Thompson (Table 4). Although the population is small and we have not found any nests, Swartz (1966) located four nests in boulder piles in 1960-1961. These records suggest Cape Thompson is the northernmost limit of breeding for this species in Alaska. Pigeon guillemots have been seen on only two occasions at Cape Lisburne and vicinity. Both sightings were of one bird each, and occurred on widely separated dates in 1977.

Horned Puffins

A complete census of horned puffins was taken in 1976 at Cape Thompson, and Colonies 1-4 were censused in 1977. Only Colony 1 was censused in 1978, the last year horned puffins were counted at one or more entire colonies at Cape Thompson. Results of our counts and data reported by Swartz (1966) for 1960 are shown in Table 5.

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Swartz (1966) compensated his counts of horned puffins for diurnal changes in numbers like he did for murres. In 1976 we made two 24-hour counts of horned puffins and compensated counts at Colonies 2, 3 and 5 on the basis of these counts. Colonies 1 and 4 were censused several times each and we have reported only the highest of all counts. Diurnal (24-h) activity counts were not made in 1977 and the numbers in Table 5 for 1977 are uncompensated scores. Likewise, the number for 1978 at Colony 1 is the uncompensated total of one count. Although these census data are not strictly comparable among years, there is no indication of large change in the number of horned puffins at Cape Thompson since 1960.

Horned puffins were censused at Cape Lisburne only in 1977 when 55 of 75 plots were counted. The total of those plots, 1,072, indicates that the number of horned puffins at Cape Lisburne is similar to the number at Cape Thompson.

The breeding cycle of horned puffins was apparently later in 1976 and 1977 than in 1960, as it was for murres, kittiwakes and gulls. We located nine nests at Cape Thompson in 1976, each of which contained one egg. Two laying dates were obtained, one between 16-20 July and another after 20 July. None of the nine eggs had hatched by 25 August. In 1977, at least one egg was laid about 15-20 July and was hatching or had just hatched on 26 August. Swartz (1966) reported two hatch dates in 1960, one on 12 August and the other between 17-20 August.

Tufted Puffins

Several complete censuses of tufted puffins were taken at Cape Thompson in 1976 and 1977, and Colony 1 was counted once in 1978. Results of our censuses are presented in Table 6, and include only the highest scores obtained during the two census years. Numbers have been consistantly small, and especially variable at Colonies 1 and 2 where the majority of pairs have nested.

We did not census tufted puffins at Cape Lisburne in 1976. The birds were generally conspicuous and there was no doubt that they were more numerous than at Cape Thompson--at least 100 individuals were apparent within the colony boundaries. In 1976 tufted puffins were also relatively numerous along the bluffs between the Cape Lisburne colony arid at Noyalik Peak where we counted about 50 individuals.

The numbers of tufted puffins at Cape Lisburne and Noyalik Peak declined sharply between 1976 and 1977. A complete census of Cape Lisburne in 1977 revealed only 11 individuals within the colony boundaries, and only 12 birds were present at Noyalik Peak.

Casual observations of tufted puffins at Cape Lisburne and Noyalik Peak in 1978-1980 indicate numbers have remained low since 1977. Only about seven individuals were seen within the colony boundaries and a few other birds were seen at Noyalik Peak in each of those years.

We cannot explain the decline in numbers of tufted puffins at Cape Lisburne and Noyalik Peak after 1977; however, both Cape Lisburne and

TABLE 1.   Numbers of active pelagic cormorant nests at Cape Thompson, 1959-1978.

Year	Colony					TOTAL
	1	2	3	4	5	
1 959[a]	1	1	0	4	0	6
1960a	3	18	0	1	1	23
1961[a]	4	18	0	1	0	23
1976	7	2	0	5	0	14
1977	16	0	0	2	0	18
1978	7	0	0	4	0	11

[a]Data are from Swartz (1966).

Cape Thompson are in the northernmost nesting range of both puffin species, and as a consequence, numbers may vary considerably from year to year. Data from Colony 1 at Cape Thompson are suggestive of this. Because of its location, Colony 1 is the most often viewed.. Tufted puffins are usually conspicuous there when they are present, because of the broad, flat rock faces and small size of the cliff, and counts there are likely to be the most accurate. In five of the six census years maximum counts varied from a low of two pairs in 1959 to a high of 12 pairs in 1976.

Nesting by tufted puffins has been confirmed only once at Cape Thompson. A single egg was found in a crevice at Colony 2 on 17 August 1976. It is likely that some pairs breed at both colonies each year. Tufted puffins are regularly seen entering and leaving crevices during July and August at both locations.

TABLE 2.   Populations of black guillemots in the vicinity of Cape
               Lisburne, 1976-1980.

Year	Cape Lisburne	Cape Lewis	Kay Creek to Noyalik Peak	Cape Lisburne to Corwin Bluff
1976	<10	NC [1]	NC	NC
1977	136-151	24	14	9
1978	108	NC	46	NC
1979	>100	NC	NC	NC
1980	154	NC	NC	56

[1]NC = no count.

TABLE 3.   Populations of pigeon and black guillemots at Cape Thompson.

Species	1959[a]	1960[a]	1961[a]	1976	1977	1978	1979
Pigeon guillemots	< 10	4	14	4-6	2'-3	--	6-8
Black guillemots	< 10	16	4	4-6	6-10 > 6		3-4

[a]Data are from Swartz (1966).

TABLE 4.   Numbers of horned puffins at Cape Thompson.

Year	Colony						Total
	0[a]	1	2	3	4	5	
1960[b]	86	418	470	210	178	540	1,902
1976	75	241	663	200	180	559	1,918
1977	65	265	344	256	142	NC[c]	---
1978	NC	218	NC	NC	NC	NC	---

[a]Colony '0' is located between colonies 1 and 2.

[b]Data are from Swartz (1966).

[c]NC = no count.

TABLE 5.   Numbers of tufted puffins at Cape Thompson.

Year	Colony					Total
	1	2	3	4	5	
1 959[a]	4	18	0	0	0	22
1960a	20	12	0	0	4	36
961[a]	6	34	0	0	0	40
976	24	13	1	0	6	4a
977	13	9	4	0	4	30
1978	10	NC[b]	NC	NC	NC	--

[a]Data are from Swartz (1966).

[b]NC = no count.

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TABLE 6. Five-minute counts of eiders flying past Cape Lisburne, 1980.

Beginning Time[1]	July					August
	27	28	29	30	31	1
1045						0
1105				0		
1230					0	
1400	750					
1440					500	
1450		500				
1500	750					
1545					300	
1810			750			
1820					300	
1940					750	
2005		100	500			
2045					500	
2140			500			
2310			0		300	

[1]Bering Daylight Time.

VIII. CONCLUSIONS

The major population decline of murres at Cape Thompson in the past two decades and the decline at Bluff since the mid-1970's might be due, at least partially, to a long series of relatively cool summers in the region when reproductive success was reduced. Although declines have occurred at Cape Thompson and Bluff, murre numbers apparently have remained stationary at Cape Lisburne and on St. Lawrence Island. Such differences among the colonies could be related to differences in proximity to concentrations of food resources.

The observed rates of decline in numbers of murres at both Cape Thompson and Bluff are greater than would be predicted on the basis of summer conditions only. Variability among counts within years is high, and therefore a single count, or the average of a few counts, provides an imprecise estimate of numbers in any particular year. Thus, the rate implied by our results may be higher than the actual rate of decline. Alternatively, the observed and actual rates could be the same, implicating factors in the wintering areas as an additional reason for the declines. Perhaps the greatest change in winter environmental conditions in the past two decades was a reduction in the winter food supply of murres due to commercial harvest of pollock. Subsequent competition for food might have resulted in increased overwinter mortality and therefore a regional decline in murre numbers. Consolidation of murres at colonies most favorably situated with respect to prey availability could have led to the apparent differences in the status of murre populations at colonies in northern Alaska.

Like murres, kittiwake numbers also changed among years, but tended to increase rather than decrease following the particularly poor breeding season of 1976. Changes in other components of their breeding biology also occurred; for example, laying dates were earlier and reproductive success increased in years following 1976. These changes and our studies of food habits of murres and kittiwakes indicated that prey availability was low in 1976 in association with unusually cold environmental conditions. A warming trend in succeeding years led to more abundant prey and much improved breeding performance of kittiwakes.

An adequate level of fish biomass is necessary for kittiwakes to enjoy good reproductive seasons. In most years a combination of Arctic cod and sand lance probably satisfies this requirement. Arctic cod stocks appear to fluctuate little by comparison to stocks of sand lance, which were essentially unavailable to kittiwakes in 1976, but increased to very high numbers by 1979. The availability of sand lance appears to be important to kittiwake chicks which grow rapidly on diets of these fish, but more slowly when sand lance are in low numbers and their diets must be supplemented with other types of food.

Although northern kittiwake populations experience years of very poor reproductive success, they also have years of very good success. Over the long term, these extremes probably balance each other and maintain the populations at more or less uniform levels.

Two basically different food webs provide most of the energy supporting seabirds in the eastern Chukchi Sea. One includes the typically Arctic taxa of cods and sculpins and their primarily benthic prey of mysids, amphipods and isopods, as well as some arctic copepods. Arctic cod and sculpins are the most abundant and widely distributed fish fauna in northern regions. The other principal food web includes sand lance and their primarily neritic, seasonal prey of boreal copepods and mero-plankton. Because sand lance form dense schools near the surface, they provide a concentrated source of energy to kittiwakes and other seabirds.

The factors responsible for maintaining these food webs are imperfectly understood. Particulate organic matter and zooplankton are advected into the Chukchi Sea by the northward flow of water from the Bering Sea. This imported energy may subsidize annual primary and secondary production north of Bering Strait and be important to food web organisms. The warming effect of Alaska Coastal Water appears to be especially important to seasonally abundant sand lance and their supporting neritic food web.

We have identified one area in the eastern Chukchi Sea that is consistently used by large numbers of a variety of seabirds and marine mammals throughout the summer. Ledyard Bay, on the north shore of the Lisburne Peninsula, provides critical feeding habitat for the majority of the birds nesting at the Cape Lisburne colonies. Moreover, large numbers of migrating eiders, non-breeding cormorants and gulls, walrus, phocid seals and gray whales are found there during much of each season. We do not fully understand the physical processes responsible for the biological richness of Ledyard Bay. The year-to-year consistency of use underscores the importance of the bay, and demonstrates a clear need to preserve the integrity of biological systems found there.

IX.   NEEDS FOR FUTURE STUDY

Murre numbers should be monitored at colonies where counts have been made in the past. We recommend that the Pribilof Islands should receive high priority because a very good census was taken there in 1975 and 1976, but not since then. The Pribilof Islands lie near the heart of the region of the pollock fishery, and murre numbers on the islands also might have declined if competition for pollock has become a significant source of winter mortality. Also, competition for pollock could lead to lowered natality of murres on the Pribilof Islands, since pollock is the main food of breeding murres there. Knowledge of the current status of murres on the Pribilof Islands would contribute greatly to our understanding of factors affecting murre numbers in northern colonies.

Studies should be resumed at the Cape Peirce-Cape Newenham colonies. Common murres attain their greatest density in this region and knowledge of their status would provide valuable counterpoint to information from the Pribilof Islands where thick-billed murres are in the vast majority.

To aid in the assessment of fisheries-seabird interactions, a colony located away from the area of possible conflict should also be investigated. Middleton Island would be a suitable site. Because it lies in the Gulf of Alaska, neither breeding nor wintering murres should be affected by activities in the Bering Sea. Moreover, the murre population on Middleton Island has increased dramatically since the mid-1950's, indicating very favorable regional environmental conditions compared to those farther north.

Low-level effort should continue at Cape Lisburne and Bluff where we now have information for six and seven consecutive years, respectively. Both sites are logistically simple and inexpensive, and the return on the investment is high. These long-term studies have been invaluable to our understanding of marine ecology in northern Alaska.

Studies of kittiwakes should be made at all sites where murres are censused. Kittiwakes are easy to work with and are very sensitive indicators of local environmental conditions.

Murres and kittiwakes should be collected at all study sites for food habits information and as a way of sampling marine organisms. An understanding of trophic relationships among seabirds and of seabird food webs is critical to any study of seabird ecology.

A program of studies that alternates among several colonies should be planned for a period of at least ten years. During that interval, each colony would be visited two or three times, and one or two colonies would be visited each year. A program of this kind would be the most efficient, accurate and precise method to monitor changes in regional ecosystems that occur naturally or in response to resource development.

X. LITERATURE CITED

Allen, P.W. and R.O. Weedfall. 1966. Weather and climate. Pp. 9-44 *in* N.J. Wilimovsky and J.N. Wolfe (eds.), Environment of the Cape Thompson region, Alaska. Div. Tech. Inf., U.S. Atomic Energy Comm., Oak Ridge, TN.

Alverson, D.L. and N.J. Wilimovsky. 1966. Fishery investigations of the southeastern Chukchi Sea. Pp. 843-860 *in* N.J. Wilimovsky and J.N. Wolfe (eds.), Environment of the Cape Thompson region, Alaska. Div. Tech. Inf., U.S. Atomic Energy Comm., Oak Ridge, TN.

Andriyashev, A.P. 1954. Fishes of the northern seas of the USSR. Akademiya Nauk SSSR, Zoological Inst. Keys to the Fauna of the USSR 53. Translated from Russian by Israel Prog. Sci. Transl. , 1964, 566 p. (Available U.S. Dept. Commerce, Nat. Tech. Info. Ser., Springfield, VA).

Asbirk, S. 1978. Tejsten Cepphus grylle som ynglefugl i Danmark. Dansk orn. Foren. Tidsskr. 72:161-178.

Bailey, E.P. and G.H. Davenport. 1972. Die-off of Common Murres on the Alaska Peninsula and Unimak Island. Condor 74:215-219.

Bakkala, R., V. Wespestad and L. Low. 1981. Pollock. Pp . 1-23 in R. Bakkala, V. Wespestad, T. Sample, R. Narita, R. Nelson, O. Ito, M. Alton, L. Low, J. Wall, and R. French. Condition of the ground fish resources of the eastern Bering Sea and Aleutian Islands region in 1981. Northwest and Alaska Fish. Center, Nat. Mar. Fish. Serv., NOAA, Seattle, WA.

Bedard, J. 1969. Feeding of the least, crested, and parakeet auklets around St. Lawrence Island, Alaska. Can. J. Zool. 47:1025-1050.

Belopolski, L.O. 1957. Ecology of colonial seabirds in the Barents Sea. Izdatel'stvo Academia Nauk SSSR, Moskva - Leningrad. 346 p.

Bent, A.C. 1919. Life histories of North American diving birds. Smithsonian Inst. U.S. Nat. Mus. Bull. 107. U.S. Govt. Printing Office, Wash. D.C. Reprinted by Dover Publ., Inc., 1963.

Bent, A.C. 1925. Life histories of North American wild fowl. Part II. Smithsonian Inst. U.S. Nat. Mus. Bull. 130. U.S. Govt. Printing Office, Wash. D.C. Reprinted by Dover Publ., Inc. 1962.

Biderman, J.O., W.H. Drury, J.B. French, Jr. and S. Hinckley. 1978. Ecological studies in the northern Bering Sea: Birds of coastal habitats on the south shore of Seward Peninsula, Alaska. Pp. 510-613 in Envir. Assess. Alaskan Cont. Shelf, Annu. Rep. Prin. Invest. , Vol. 2. BLM/NOAA OCSEAP, Boulder, CO.

Birkhead, T.R. 1974 . Movements and mortality rates of British guille-roots. Bird Study 21:241-254.

Birkhead, T.R. 1977. The effect of habitat and density on breeding success in the common guillemot *(Uris aalge)*. J. Anim. Ecol. 46:751-764.

Birkhead, T.R. 1978a. Attendance patterns of guillemots *Uris aalge* at breeding colonies on Skomer. Ibis 120:219-229.

Birkhead. T.R. 1978b. Behavioral adaptations to high density nesting in the common guillemot *Uria aalge*. Anim. Behav. 26:321-331.

Birkhead, T.R. and P.J. Hudson. 1977. Population parameters for the common guillemot *Uris aalge*. Ornis Stand. 8:145-154.

Birkhead, T.R. and D.N. Nettleship. 1980. Census methods for murres, *Uris* species: a unified approach. Can. Wildl. Serv. Occas. Pap. No. 43.

Birkhead, T.R. and D.N. Nettleship. 1981. Reproductive biology of Thick-billed murres *(Uria lomvia)*: an intercolony comparison. Auk 98: 258-269.

Blackburn, J.E., K. Anderson, C.I. Hamilton and S.J. Starr. 1981. Pelagic and demersal fish assessment in the lower Cook Inlet estuary system. Pp. 259-602 *in* Envir. Assess. Alaskan Cont. Shelf, Final Rep. Prin. Invest., Vol. 12. BLM/NOAA OCSEAP, Boulder, CO.

Bloom, G.L. 1964. Water transport and temperature measurements in the eastern Bering Strait, 1953-1958. J. Geophys. Res. 69:3335-3354.

Bradstreet, M.S.W. 1980. Thick-billed murres and black guillemots in the Barrow Strait area, N.W.T. during spring: diets and food availability along ice edges. Can. J. Zool. 58:2120-2140.

Brown, R.G.B. 1980. Seabirds as marine animals. Pp. 1-39 *in* J. Burger, B.L. Olla, and H.E. Winn (eds.), Behavior of marine animals, Vol. 4. Plenum, New York.

Campbell, R.H. 1966. Areal geology. Pp. 57-84 *in* N.J. Wilimovsky and J.N. Wolfe (eds.), Environment of the Cape Thompson region, Alaska. Div. Tech. Inf., U.S. Atomic Energy Comm., Oak Ridge, TN.

Coachman, L.K., K. Aagaard and R.B. Tripp. 1975. Bering Strait, the regional physical oceanography. Univ. Wash. Press, Seattle, WA. 172 p.

Coachman, L.K. and R.L. Charnell. 1979. On lateral water mass interaction -- a case study, Bristol Bay, Alaska. J. Phys. Oceanog. 9:278-297.

Coachman, L.K. and K. Aagaard. 1981. Re-evaluation of water transports in the vicinity of Bering Strait. Pp. 95-100 *in* D.W. Hood and J.A. Calder (eds.), The eastern Bering Sea shelf: oceanography and resources, Vol. 1. Office of Marine Pollution Assess. , NOAA, U.S. Dept. Commerce.

Conover, W.J. 1980. Practical nonparametric statistics. .Wiley, New York.

Cooney, R.T. 1981. Bering Sea zooplankton and micronecton communities with emphasis on annual production. Pp. 947-974 *in* D.L. Hood and J.A. Calder (eds.), The eastern Bering sea shelf: oceanography and resources, Vol. 2. Office of Marine Pollution Assess. , Nat. Oceanic Atmos. Admin., U.S. Dept. Commerce.

Cooney, R.T. and K. Coyle. MS. Trophic implications of cross-shelf copepod distributions in the southeastern Bering Sea.

Coulson, J.C. 1963. Egg size and shape in the kittiwake *(Rissa tridactyla)* and their use in estimating age composition of populations. Proc. Zool. Sot. Lend. 140:211-227.

Coulson, J.C. and J.M. Horobin. 1972. The annual re-occupation of breeding sites by the Fulmar. Ibis 114:30-42.

Coulson, J.C. and E. White. 1958. The effect of age on the breeding
    biology of the kittiwake *Rissatridactyla*. <u>Ibis</u> 100:40-51.

Coulson, J.C. and R.D. Wooler. 1976. Differential survival rates among
    breeding kittiwake gulls. <u>J. Anim. Ecol.</u> 45:205-213.

Craig, P.C. and L. Haldorson. 1981. Part 4. Fish. P. 384-678 <u>in</u> S.R.
    Johnson and J.W. Richardson (eds.), Beaufort Sea barrier island –
    lagoon ecological process studies: Final report, Simpson Lagoon.
    Envir. Assess. Alaskan Cont. Shelf, Final Rep. Prin. Invest. , Vol.
    7. BLM/NOAA OCSEAP, Boulder, CO.

Cramp, S., W.R.P. Bourne and D. Saunders (eds.). 1974. The seabirds of
    Britian and Ireland. Collins, London.

Cushing, D.H. and R.R. Dickson. 1976. The biological response in the
    sea to climatic changes. <u>Adv. Mar. Biol.</u> 14:1-22.

DeGange, A.R. 1978. Observations on the mortality of seabirds in Japan-
    ese salmon gillnets made from the Oshoro Maru and Hokusei Maru,
    Summer 1978. U.S.F.W.S. , Office Biol. Serv. – Coastal Ecosystems.
    Anchorage, AK.

Dickson, R.R. and J. Namias. 1979. Atmospheric climatology and its
    effect on sea surface temperature - 1976. Pp. 19-33 *in* J.R. Goulet,
    Jr. and E.D. Haynes (eds.), Ocean Variability in the U.S. Fishery
    Conservation Zone. NOAA Tech. Rep., Nat. Marine Fish. Serv. Circ.
    No. 427, U.S. Dept. Commerce.

Divoky, G.J. 1978. The distribution, abundance and feeding ecology of
    birds associated with pack ice. *in* Envir. Assess. Alaskan Cont.
    Shelf, Annu. Rep. Prin. Invest., Vo. 2. BLM/NOAA OCSEAP, Boulder,
    co.

Divoky, G.J. 1978. The distribution, abundance and feeding ecology of
    birds associated with pack ice. Pp. 167-509 *in* Envir. Assess.
    Alaskan Cont. Shelf, Annu. Rep. Prin. Invest., Vol. 12. BLM/NOAA
    OCSEAP, Boulder, CO.

Divoky, G.J., G.E. Watson and J.C. Bartonek. 1974. Breeding of the
    black guillemot in northern Alaska. Condor 76:339-343.

Drury, W.H. 1979. Population dynamics of northern marine birds. Pp.
    123-140 *in* J.C. Bartonek and D.N. Nettleship (eds.), Conservation
    of marine birds of northern North America. U.S. Fish Wildl. Serv.,
    Wildl. Res. Rep. 11.

Drury, W.H. and I.C.T. Nisbet. 1972. The importance of movements in the
    biology of herring gulls in New England. Pp. 173-212 *in* Population
    ecology of migratory birds: a symposium. U.S. Fish, Wildl. Serv.
    Wildl. , Res. Rep. 2.

Drury, W.H., C. Ramsdell and J.B. French, Jr. 1981. Ecological studies in the Bering Straits region. Pp. 175-488 *in* Envir. Assess. Alaskan Cont. Shelf, Final Rep. Prin. Invest. , Vol. 11. BLM/NOAA OCSEAP, Boulder, CO.

Fleming, R.H. and D. Heggarty. 1966. Oceanography of the southeastern Chukchi Sea. Pp. 697-754 *in* N.J. Wilimovsky and J.N. Wolfe (eds.), Environment of the Cape Thompson region, Alaska. Div. Tech. Inf., U.S. Atomic Energy Comm., Oak Ridge, TN.

Flock, W.L. 1973. Radar observations of bird movements along the Arctic coast of Alaska. Wilson Bull. 85:259-275.

Fretwell, S.D. 1972. Populations in a seasonal environment. Monogr. Pop . Biol. 11. Princeton Univ. NJ.

Frost, K.J. and L.F. Lowry. 1981. Trophic importance of some marine gadids in northern Alaska and their body-otolith size relationships. Fishery Bull. 79:187-192.

Furness, R.W. 1978. Energy requirements of seabird communities: a bioenergetic model. J. Anim. Ecol. 47:39-53.

Gould, P.J. 1977. Shipboard surveys of marine birds. Pp. 193-254 *in* Envir. Assess. Alaskan Cont. Shelf, Annu. Rep. Prin. Invest. , Vol. 3. BLM/NOAA OCSEAP, Boulder, CO.

Gulland, J.A. 1978. Review of the state of world fishery resources. FAO Fish. Circ. No. 710. FAO, Rome. 42 p.

Harrison, C.S. 1977. Aerial surveys of marine birds. Pp. 285-593 *in* Envir. Assess. Alaskan Cont. Shelf, Annu. Rep. Prin. Invest. , Vol. 3. BLM/NOAA OCSEAP, Boulder, CO.

Hatch, S.A., T.W. Pearson and P.J. Gould. 1979. Reproductive ecology of seabirds at Middleton Island, Alaska. Pp. 233-308 *in* Envir. Assess. Alaskan Cont. Shelf, Annu. Rep. Prin. Invest. , Vol. 2. BLM/NOAA OCSEAP, Boulder, CO.

Hufford, G.L. 1973. Warm water advection in the southern Beaufort Sea, August-September 1971. J. Geophys. Res. 78:2702-2707.

Hunt, G.L. Jr., B. Burgeson and G.A. Sanger. 1981. Feeding ecology of seabirds of the eastern Bering Sea. P. 629--647 *in* D.W. Hood and J.A. Calder (eds.), The eastern Bering Sea shelf: oceanography and resources, Vol. 2. Office of Marine Pollution Assess. NOAA, U.S. Dept. Commerce.

Hunt, G.L., Jr., Z. Eppley, B. Burgeson and R. Squibb. 1981. Reproductive ecology, food and foraging areas of seabirds nesting on the Pribilof Islands, 1975-1979. Pp. 1-257 *in* Envir. Assess. Alaskan Cont. Shelf, Final Rep. Prin. Invest. , Vol. 12. BLM/NOAA OCSEAP, Boulder, CO.

Ingham, M.C., B.A. Rutland, P.W. Barnes, G.E. Watson, G.J. Divoky, A.S. Naidu, G.D. Sharma, B.L. Wing and J.C. Quast. 1972. An ecological survey in the eastern Chukchi Sea. U.S. Coast Guard Oceanog. Rep. No. 50, CG 373-50., Wash. D.C. 206 p.

Ingraham, W.J., Jr. 1981. Shelf environment. pp. 455-469 *in* D.W. Hood and J.A. Calder (eds.), The eastern Bering Sea shelf: oceanography and resources, Vol. 1. Office of Marine Pollution Assess., NOAA, U.S. Dept. Commerce.

Inoue, A., S. Takamori, K. Kuniyaki, S. Kobayashi and S. Nishina. 1967. Studies on fishery biology of the sand lance, *Ammodytes personatus* (Girard). Bull. Naidai Reg. Fish. Res. Lab. 25:1-335.

Irving, L. C.P. McRoy and J.J. Burns. 1970. Birds observed during a cruise in the ice-covered Bering Sea in March 1968. Condor 72:110-112.

Iverson, R.L., L.K. Coachman, R.T. Cooney, T.S. English, J.J. Goering, G.L. Hunt, Jr., M.C. Macauley, C.P. McRoy, W.S. Reeburg and T.E. Whitledge. 1979. Ecology significance of fronts in the southeastern Bering Sea. Pp. 437-466 *in* R.J. Livingston (cd.), Ecological processes in coastal and marine systems. Plenum, New York.

Johnson, C.M. 1980. Wintertime Arctic sea ice extremes and the simultaneous atmospheric circulation. Monthly Weather Review 108:1782-1791.

Johnson, M.W. 1956. The plankton of the Beaufort and Chukchi sea areas of the Arctic and its relation to the hydrography. Arctic Inst. North Amer. Tech. Paper No. 1, Montreal. 32 p.

Johnson, R.A. 1938. Predation of gulls in murre colonies. Wilson Bull. 50:161-170.

Johnson, S.R., W.J. Adams and M.R. Morrell. 1975. The birds of the Beaufort Sea. Unpubl. Rep. by LGL Limited Environ. Res. Assoc., Edmonton, Alberta for the Can. Wildl. Serv., Edmonton, Alberta. 310 p.

Kinder, T.H., G.L. Hunt, Jr., D. Schneider and J.D. Schumacher. MS. Correlations between seabirds and oceanic fronts around the Pribilof Islands, Alaska.

King, W.B., R.G.B. Brown and G.A. Sanger. 1979. Mortality to marine birds through commercial fishing. Pp. 195-199 *in* J.C. Bartonek and D.N. Nettleship (eds.), Conservation of marine birds of northern North America. U.S. Fish. Wildl. Serv. Wildl. Res. Rep. 11.

Lloyd, C. 1975. Timing and frequency of census counts of cliff-nesting auks. Brit. Birds 68:503-513.

Lowry, L.F. and K.J. Frost. 1981. Distribution, growth, and foods of Arctic cod *(Boreogadus saida)* in the Bering, Chukchi and Beaufort seas. Can. Field-Nat. 95:186-191.

Macy, P.T., J.M. Wall, N.D. Lampsakis and J.E. Mason. 1978. Resources of non-salmonid pelagic fishes of the Gulf of Alaska and eastern Bering Sea. Unpub 1. rep., Nat. Marine Fish. Serv., NOAA. Seattle, WA.

Maunder, J.E. and W. Threlfall. 1972. The breeding biology of the black-legged kittiwake in Newfoundland. Auk 89:789-816.

McRoy, C.P. and J.J. Goering. 1976. Annual budget of primary production in the Bering Sea. Marine Sci. Commun. 2:255-267.

McRoy, C.P., J.J. Goering and W.E. Shiels. 1972. Studies of primary productivity in the eastern Bering Sea. Pp. 199-216 *in* A.Y. Takemouti *et al.* (eds.), Biological oceanography of the northern North Pacific Ocean. Idemitsu Shoten, Tokyo.

Mertz, D.B. 1971. The mathematical demography of the California Condor population. Amer. Natur. 105:437-453.

Namias, J. and D.R. Cayan. 1981. Large-scale air-sea interactions and short-period climatic fluctuations. Science 214:869-876.

Nelson, R.K. 1969. Hunters of the northern ice. Univ. Chicago Press. 168 p.

Nettleship, D.N. 1977. Seabird resources of eastern Canada: Status, problems and prospects. Pp. 96-108 *in* T. Mosquin and C. Suchal (eds.), Proceedings of the symposium of Canada's threatened species and habitats. Can. Wildl. Fed., Ottawa.

Niebauer, H.J. 1980. Sea ice and temperature variability in the eastern Bering Sea and the relation to atmospheric fluctuations. J. Geophys. Res. 85:7507-7515.

Niebauer, H.J. 1981a. Recent short-period wintertime climatic fluctuations and their effect on sea-surface temperatures in the eastern Bering Sea. Pp. 23-30 *in* D.W. Hood and J.A. Calder (eds.), The eastern Bering Sea shelf: oceanography and resources, Vol. 1. Office of Marine Pollution Assess. , NOAA, U.S. Dept. Commerce.

Niebauer, H.T. 1981b. Recent fluctuations in sea ice distribution in the eastern Bering Sea. Pp. 133-140 *in* D.W. Hood and J.A. Calder (eds.), The eastern Bering Sea shelf: oceanography and resources, vol. 1. Office of Marine Pollution Assess. , NOAA, U.S. Dept. Commerce.

Pearson, T.H. 1968. The feeding biology of sea-bird species breeding on the Fame Islands, Northumberland. J. Anim. Ecol. 37:521-551.

Perrins, C.M. 1970. The timing of birds' breeding seasons. Ibis 112: 242-255.

Pitt, T.K. 1958a. Age and growth of the capelin, *Mallotus villosus* (Muller), from Newfoundland and Grand Bank areas. J. Fish. Res. Bd. Canada 15:295-311.

Pitt, T.K. 1958b. Distribution, spawning and racial studies of the capelin, *Mallotus villosus* (Muller), in the offshore Newfoundland area. J. Fish. Res. Bd. Canada 15:275-293.

Ramsdell, C. and W.H. Drury. 1979. Ecological studies of birds in the northern Bering Sea. Pp. 600-769 *in* Envir. Assess. Alaskan Cont. Shelf, Annu. Rep. Prin. Invest. , Vol. 1. BLM/NOAA OCSEAP, Boulder, CO.

Reay, P.J. 1972. The seasonal pattern of otolith growth and its application to back-calculation studies in *Ammodytes tobianus*. L.J. Cons. Int. Explor. Mer 34:485-504.

Redburn, D.R. 1974. The ecology of the inshore marine zooplankton of the Chukchi Sea near Point Barrow, Alaska. M.Sc. Thesis. Univ. Alaska, Fairbanks, AK. 171 p.

Rogers, D.E., D.J. Rabin, B.J. Rogers, K. Garrison and M. Wangerin. 1979. Seasonal composition and food web relationships of marine organisms in the nearshore zone of Kodiak Island--including ichthyoplankton, meroplankton (shellfish), zooplankton and fish. Pp. 529-662 *in* Envir. Assess. Alaskan Cont. Shelf, Annu. Rep. Prin. Invest., Vol. 4. BLM/NOAA OCSEAP, Boulder, CO.

Runde, O.J. and R.T. Barrett. 1981. Variations in egg size and incubation period of the kittiwak *Rissa tridactyla* in Norway. Ornis Stand. 12:80-86.

Schaefer, M.B. 1970. Men, birds and anchovies in the Peru Current - dynamic interactions. Trans. Amer. Fish. Sot. 99:461-467.

Searing, G. 1977. Some aspects of the ecology of cliff-nesting seabirds at Kongkok Bay, St. Lawrence Island, Alaska, during 1976. Pp. 263-412 *in* Envir. Assess. Alaskan Cont. Shelf, Annu. Rep. Prin. Invest. , vol. 5. BLM/NOAA OCSEAP, Boulder, CO.

Shumacher, J.D., T.H. Kinder, D.J. Pashinski and R.L. Charnell. 1979. A structural front over the continental shelf of the eastern Bering Sea. J. Phys. Oceanog. 9:79-87.

Shuntov, V.P. 1974. Seabirds and the biological structure of the ocean. Natl. Tech. Info. Serv., U.S. Dept. Commerce. TT-74-55032, transl. from Russian Dalnevostochnoe knizhnoe izdatelstvo, Vladivostok, 1972.

Slater, P.J.B. 1980. Factors affecting the numbers of guillemots *Uris aalge* present on cliffs. <u>Ornis Stand.</u> **11:155-163.**

Sowls, A.L., S.A. Hatch and C.J. Lensink. 1978. Catalog of Alaskan seabird colonies. **Biol.** Serv. **Prog.,** U.S. Fish. **Wildl.** Serv., Anchorage, Alaska. 251 p.

Spring, L. 1971. A comparison of functional and morphological adaptations in the common murre *(Uris aalge)* and thick-billed murre *(Uris lomvia).* <u>Condor</u> **73:1-27.**

Springer, A.M., **D.G.** Roseneau and M. Johnson. 1979. Ecological studies of colonial seabirds at Cape Thompson and Cape **Lisburne,** Alaska. Pp. 517-574 *in* Envir. Assess. Alaskan Cont. Shelf, Annu. Rep. Prin. Invest. , Vol. 2. BLM/NOAA OCSEAP, Boulder, CO.

Steele, **B.B.** and **W.H.** Drury. 1977. Birds of coastal habitats on the south shore of the Seward Peninsula, Alaska. Pp. 1-178 *in* **Envir.** Assess. Alaskan Cont. Shelf, **Annu.** Rep. Prin. Invest. , Vol. 3. BLM/NOAA OCSEAP, Boulder, CO.

Stoker, S. 1981. Benthic invertebrate **macrofauna** of the eastern **Bering/Chukchi** continental shelf. Pp. 1069-1090 *in* **D.W.** Hood and **J.A. Calder** (eds.), The eastern Bering Sea shelf: oceanography and resources, Vol. 2. Office of Marine Pollution Assess., NOAA, U.S. Dept. Commerce.

Straty, **R.R.** and **R.E.** Haight. 1979. Interactions among marine birds and commercial fish in the eastern Bering Sea. Pp . 201-220 *in* J.C. Bartonek and **D.N.** Nettleship **(eds.),** Conservation of mairne birds of northern North America. U.S. Fish **Wildl.** Serv. **Wildl.** Res. Rep. 11.

Swartz, **L.G.** 1966. Sea-cliff birds. Pp. 611-678 *in* **N.J. Wilimovsky** and **J.N.** Wolfe **(eds.),** Environment of the Cape Thompson region, Alaska. Div. Tech. **Inf.,** U.S. Atomic Energy **Comm.,** Oak Ridge, TN,

Swartz, **L.G.** 1967. Distribution and movements of seabirds in the Bering and **Chukchi** Seas. <u>Pacific Science</u> 21:332-347.

Thompson, **D.Q.** and **R.A.** Person. 1963. The eider pass at Point Barrow, Alaska. <u>J. Wild. Man.</u> **27:348-355.**

Tull, **C.E.** and P. **Germain.** 1972. Mortality of thick-billed **murres** in the West Greenland salmon fishery. <u>Nature</u> **237(5349):42-44.**

Vesin, J.P., **W.C.** Leggett and **K.W.** Able. 1981. Feeding ecology of capelin *(Mallotus villosus)* in the estuary and western Gulf of St. Lawrence and its **multispecies** implications. <u>Can. J. Fish.</u> <u>Aqua. Sci.</u> **38:257-267.**

Walsh, J.E. and C.M. Johnson.   1979.   An analysis of Arctic sea ice
    fluctuations, 1953-77.   J. Phys. Oceanog. 9:580-591.

Warner, I.M.   1981.   Capelin - a part of Alaska's future.   Alaska Seas
    and Coasts 9:4-7.

Williams, A.J.   1974 .   Site preferences and interspecific competition
    among guillemots Uris aalge (L.) and Uria lomvia (L.) on Bear Island.
    Ornis Stand. 5:113-121.

Williamson, F.S.L., M.C. Thompson and J.Q. Hines.   1966.   Avifaunal
    investigations.   Pp. 437-480 in N.J. Wilimovsky and J.N. Wolfe
    (eds.), Environment of the Cape Thompson region, Alaska. Div.
    Tech. Inf., U.S. Atomic Energy Comm., Oak Ridge, TN.

Wing, B.L. 1974.   Kinds and abundance of zooplankton collected by USCG
    icebreaker GLACIER in the eastern Chukchi Sea, Sept.-Ott. 1970.
    NOAA, Nat. Marine Fish. Serv. Tech. Rep. No. SSRF-679, U.S. Dept.
    Commerce.

Winslade, P.   1974.   Behavioral studies on the lesser sandeel Ammodytes
    marinus (Raitt) 111.   The effect of temperature on activity and
    the environmental control of the annual cycle of activity.   J. Fish.
    Biol. 6:587-599.

Winters, G.H.   1981.   Growth patterns in sand lance, Ammodytes dubius,
    from the Grand Bank.   Can. J. Fish. Squat. Sci. 38:841-846.

Zar, J.H.   1974.   Biostatistical analysis.   Prentice-Hall.   Englewood
    Cliffs, New Jersey.